













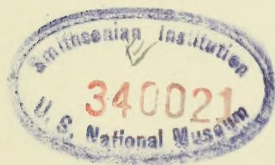


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# The Great Basin Naturalist

Volume IV, 1943

VASCO M. TANNER, *Editor*



PUBLISHED AT PROVO, UTAH, BY  
THE DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY  
OF BRIGHAM YOUNG UNIVERSITY

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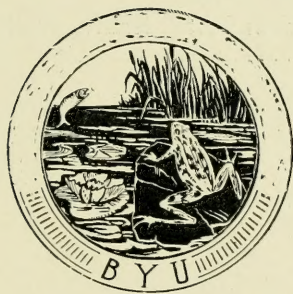
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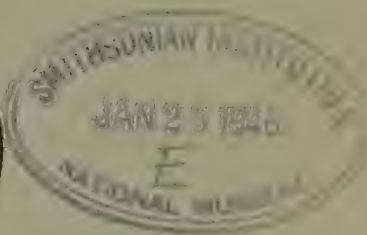
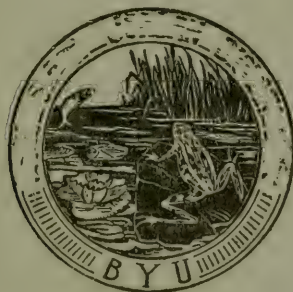
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# The Great Basin Naturalist

VASCO M. TANNER, *Editor*

C. LYNN HAYWARD, *Assistant Editor*

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# The Great Basin Naturalist

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VOLUME VI

NOVEMBER 15, 1945

Nos. 1-4

## BIOTIC COMMUNITIES OF THE SOUTHERN WASATCH AND UINTA MOUNTAINS, UTAH <sup>(1)</sup>

C. LYNN HAYWARD <sup>(2)</sup>

Associate Professor of Zoology  
Brigham Young University

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(1) Contribution from the Department of Zoology, University of Illinois and number 108 from the Department of Zoology and Entomology, Brigham Young University.

(2) This paper is part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Illinois.

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## I. INTRODUCTION

### A. SCOPE AND NATURE OF PROBLEM

Certain similarities between boreal and montane faunas and floras in North America were pointed out long ago by Merriam (1890) Coville (1893) and Rydberg (1900) and have been alluded to by many workers before and since that time. In the organization of biotic communities along the lines of modern bio-ecological procedure there would appear to be little doubt that the extensive coniferous forests, characteristic of mountainous parts of Western North America, belong to the same biotic unit as the vast expanse of transcontinental woods extending across the provinces of Canada. The evidence for such a position lies partly in the existence of a number of specifically identical or ecologically equivalent organisms which occur throughout the greater part of the whole area; but there is also a similarity in life form and life habits of the constituents, associated with affinities of habitat and climate, that gives character and unity to the whole community.

Shelford and Olsen (1935) considered the transcontinental forests as a biome (Picea-Abies Biome) and suggested (p. 397) that the

mountain forests might be included as associations in the same biome. Weaver and Clements (1938, p. 481), on the basis of plants, placed the mountainous forests in two distinct formations (Montane Forest and Subalpine Forest) distinct from the transcontinental forests which were also subdivided into three communities of formational rank. From the point of view of both animals and plants, as well as more general features of life form, life habits and climate, such an arrangement would seem unjustifiable.

Rasmussen (1941) in his studies of the Kaibab Plateau of Arizona saw the close relationship of these two communities and combined them under the general term "Montane Forest." Furthermore he reduced the formations of Clements to associational rank under the terms *Pinus brachyptera-Sciurus kaibabensis* Association, and *Picea-Abies-Sciurus fremonti* Association. From the writer's studies in the Wasatch and Uinta Mountains the thesis of Rasmussen would seem entirely justifiable.

However, it is here proposed that the Transcontinental Coniferous Forest Biome of Shelford and Olsen (see op. cit.) be expanded to the Transcontinental-Montane Coniferous Forest Biome. The term "Montane Forest" is used in a geographical sense to indicate the mountainous part of the biome, just as the term "Transcontinental Forest" refers to the lowland part, and does not necessarily represent a biotic unit.

It is further proposed that the Montane Forest of the Rocky Mountains be subdivided into two communities of associational rank known as the Lower Montane Forest (*Pinus ponderosa-Pseudotsuga mucronata-Abies concolor* Association), and the Upper Montane Forest (*Picea engelmanni-Abies lasiocarpa* Association). This nomenclature agrees in the main with that of Rasmussen (op. cit.) except that the animal constituents are left out of the community names. It would seem to the writer to be less confusing to designate these communities by plants of wide distribution rather than by animal species which often are limited to comparatively small areas such as the Kaibab squirrel, for example.

Justification for separating the Montane Forest into two associations comes primarily from differences in the dominant and subdominant vegetation and only secondarily from the few animals that are confined to one or the other. The above classification pertains only to the Rocky Mountains portion of the Montane Forest since the Sierran and Coastal Forests are not included in the study. It seems likely that these forests will fall into two or more additional associations based

also primarily upon floristic differences associated with climate. The works of Grinnell (1930) Merriam (1899) and others bear out the general faunistic relationships of these more western mountain ranges with the transcontinental forests.

Comparison of partial lists of plants and animals known from the Transcontinental Forests with partial lists from the Montane Forests represented in this study shows that at least 98 forms have specifically identical or ecological equivalent species occurring throughout the two areas. These include most of the dominant and major influent organisms that are of greatest importance in the evaluation of biotic communities. This list includes only 31 species of invertebrates, and would undoubtedly be greatly expanded if the distribution of these lower forms were better known.

The bio-ecological relationships between the alpine and arctic communities are less evident as will be shown in more detail in the part of this paper dealing with the alpine of Mt. Timpanogos.<sup>(3)</sup>

#### B. METHODS

The present study has been carried forward by the writer intermittently over a period of approximately 11 years. During the summer of 1930 a period of about six weeks (July 1 to August 15) was spent in the Trial and Mirror Lake regions of the western Uinta Mountains making studies and collections of the alpine and upper montane birds of that area. A portion of the results of this study was later published (1931). Most of the field work in the southern Wasatch has been done on Mt. Timpanogos and nearby areas. The writer's first work on Mt. Timpanogos was carried out during a six week's period from the middle of July to the last of August, 1933, at which time he was on the faculty of the Brigham Young University Alpine Summer School. Due to teaching obligations it was possible to make only general observations on the fauna and flora at this time; but at the close of the period there was drawn up a tentative plan for carrying out an investigation of the biotic communities of the mountain. The essence of this working outline has been carried forward when opportunity has afforded, to the present time.

During the following summer (1934) it was possible to spend a period from June 8 to June 21 in continuous field work on Mt. Timpanogos. This work was mostly qualitative in nature, but a considerable collection of invertebrates and a few vertebrates was made.

(3) Since this paper went to press an important paper by R. F. Daubenmire on "Vegetational Zonation in the Rocky Mountains" (*The Bot. Rev.*, 9 (6): pp. 393, 1943) has come to the writer's attention. It is regrettable that this work could not receive more attention at this time.



No field work was done in the area in 1935, and in 1936 only a few visits to Mt. Timpanogos were possible. However, the entire summer of 1937, from June 5 to August 12 was spent in continuous field work on Mt. Timpanogos and adjacent portions of the Wasatch and Uinta Mountains. The first part of this summer (June 5-July 15) was spent on Mt. Timpanogos, when a series of the smaller mammals of the area was trapped and preserved for identification purposes. The latter part of the season to August 15 was spent making a general reconnaissance trip which carried the writer and Mr. James Bee, a student assistant, into the Uinta Basin, then across the east end of the Uinta Mountains by way of the Vernal-Manilla road to Fort Bridger, Wyoming. Later in the season some field work was done in the Bear River Range in southeastern Idaho. The latter range is the northernmost spur of the Wasatch. During this period observations and collections were made principally of birds and mammals.

During portions of the summers of 1938, 1939, 1940, and 1941, field work was continued at selected stations on Mt. Timpanogos and in the Uinta Mountains. The periods during which the work was carried forward were as follows: 1938, August 1 to September 1; 1939, August 8 to September 8; 1940, June 1 to September 5; 1941, June 1 to August 20. General observations only were possible during the latter part of the 1941 season.

In addition to these more or less continuous periods spent in the field, many week-ends and holidays at all seasons of the year were devoted to this work.

Studies in areas somewhat remote from the region herein considered have also contributed indirectly to the problem at hand. These have included a brief period in the Colorado Rocky Mountains during the summer of 1932; a six week's period in the La Sal Mountains of Grand and San Juan Counties, Utah, during the summer of 1934 (see Tanner and Hayward, 1934), a short period in the high plateau region of the south-central Utah in 1936, and a six week's period from June 23 to July 28, 1939, with the animal ecology class from the University of Illinois in the north woods, tundra, grasslands and Rocky Mountains of Canada.

During the early part of the study the collections and observations made were principally of a qualitative nature. Quantitative studies were begun in 1938, but since the methods used were not the same as those adopted in the later years, the data are not strictly comparable and are not here used except in a general way to indicate populations.

The field work carried out in 1938 to 1941 consisted of two major divisions: namely, general observations and routine quantitative sampling. Due to the fact that a number of the stations were far removed from one another and the transportation of equipment difficult, it was not possible to sample each station as often as would be desirable. It is felt that the data on invertebrates, especially, was not taken at frequent enough intervals to give a true picture of seasonal population changes.

Small mammal samples (animals of chipmunk size and smaller) were taken on square plots of one half acre or 0.2 hectare. One hundred small snap traps were set in this area generally in rows about 12 feet apart. However, the rows were not strictly followed where favorable places were noted elsewhere. The traps were baited with oatmeal and were visited and reset where necessary in early morning and late evening. Each plot was trapped for four or five consecutive days, which was generally sufficient to trap out most of the small mammals.

It would appear to the writer that the data gathered by this method is of value chiefly in a comparative way and should not be relied upon to give an accurate picture of the actual mammal population of any area. Nevertheless, these comparative data, when obtained in a uniform manner, are of great value in evaluating a community; and, in comparative studies such as this, afford at least a working basis for the analysis of populations. A number of possible errors are at once apparent when such a system is used to obtain the total small mammal population of any area. First, the error resulting from influx and efflux is almost impossible to estimate. Dice (1938) has proposed formulae for correction of this error, but these formulae assume a knowledge of the home range of each species, and such data are generally not available for the smaller mammals. Other workers suggest the use of circular plots to reduce the boundary distance and thus decrease the error. Such plots, however, are not practicable in certain types of vegetation such as chaparral, and, even so, the error of efflux and influx must still be considerable. The general shyness of some mammals, and preference for different kinds of bait may be of considerable importance in this connection, although this generally applies to the less abundant species.

Various devices were used for estimation of the populations of the larger mammals, but on the whole great difficulty was encountered in arriving at accurate figures. Numbers of mule deer, which is fairly abundant in the Mt. Timpanogos area were difficult to estimate because of the fact that most of the area is steep and clothed with a dense

growth of chaparral and trees. The grazing of sheep over the greater part of the mountain tended to obliterate and confuse "signs" which otherwise might have been useful in arriving at comparative numbers.

Very few of the larger predatory animals remain in the areas studied and those present are being rapidly destroyed by man. A few direct observations on bear, bobcats, coyotes, as well as records from reliable sources gave some indications of the relative numbers of these mammals.

Relative numbers of large and medium sized rodents of above chipmunk size were arrived at by counting scat, burrows, mounds, nests and general signs, and also by cruising.

Bird populations were estimated by means of cruising over measured areas usually five acres or 2 hectares in extent. The shape and dimensions of these areas varied with the topography and vegetation. The counts showed rather uniform results when made during periods of population stability, and were felt to be quite satisfactory for most of the stations. Some difficulty was encountered in bird census work in the chaparral. This type of vegetation is so dense and harsh that it is almost impossible to penetrate, and the station studied occurred on a very steep hillside. In addition, the birds that inhabit this community are generally secretive and often quiet. In this situation, therefore, it was found necessary to select some lookout where a small area of known size could be watched and then take note of the bird activity over a long period. This system, while fairly effective during the breeding season, was not so useful at other seasons when the birds feed quietly on the ground and seldom come to the tops of the shrubs.

In order to keep the results of the bird census work as uniform as possible the counts were made at uniform times, six to seven o'clock mornings and evenings. The morning counts generally were higher, and were taken, therefore, to represent the nearest approximation of the actual population.

Invertebrate samples were taken by means of random sampling in the top two inches of soil and leaf litter, and in herb, shrub, and trees, or whatever portion of these layer communities obtained in a given community. In making the ground studies a tenth square meter of soil was removed, placed in a paper bag and then carefully sorted for animals. Invertebrates of the vegetation were sampled by taking 48-50 sweeps with a net having a diameter of 30 centimeters. This is taken to represent one square meter following the same method used by Weese (1924), Bird (1930), and Rasmussen (1941).

## C. REVIEW OF PREVIOUS WORK

Aside from work on surrounding regions which has a bearing upon the study at hand, comparatively little published material is available regarding the portions of the Wasatch and Uinta Mountains here considered. This is especially true of the Mt. Timpanogos section. As far as the writer is aware the only published works bearing directly upon the vertebrates of this mountain are a short paper by Tanner on the mammals (1927) and two brief papers on the birds by Hayward (1935a, 1941). Records of invertebrates found on Mt. Timpanogos appear in numerous publications; but no work of which the writer is aware deals exclusively with this group of animals in the area except for a list of the aphids published by Knowlton (1942).

The plant ecology of Timpanogos Creek has been studied by Harris (1926); and Flowers (1926) has worked out a comprehensive treatment of the mosses of the mountain. Neither of these reports has been published, but they are available in manuscript form.

The Uinta Mountains are much better known biologically, judging from the number of papers that have appeared dealing with that region. Aside from the earlier topographical and geological surveys of the Uinta Mountains which include some reference to the plants and animals, a number of major and minor studies have been made on the biota of the region. Svihla (1931, 1932) has discussed the mammals particularly of the eastern portion of the range. Tanner (1931a) has studied many of the lakes and streams of the area. Nelson (1875, pp. 343-345) spent a few days in the Uinta Mountains 30 miles south of Fort Bridger and listed 27 species of birds from the area; and Hayward (1931) listed 36 species of birds from high elevations in the vicinity of Trial and Mirror Lakes. A party from the Carnegie Museum including J. K. Doult and A. C. Twomey, mammalogist and ornithologist respectively, studied and collected extensively in the Uinta Basin and Uinta Mountains during the summer of 1937. Twomey's paper (1942) is now in print, but Mr. Doult's work has not as yet been published. In addition there are a number of minor references to birds and mammals of the Uinta Mountains recorded in the literature.

Pammell (1903, 1913) and Cottam (1929, 1930) have both contributed to our botanical knowledge of the Uinta Mountains; but the most comprehensive treatment of the flora is that of Graham (1937) resulting from extensive field work from 1931 to 1936. This work has been of great value in the present study.

No attempt has been made to search the literature for all of the



species of invertebrates recorded from the area studied. The study is confined rather to those organisms that the writer has been able to personally see and study. Most of the faunistic lists found in the literature are of little use in an ecological study since there is seldom any information as to exact habitats, relative numbers and other relationships.

At least three studies of a bio-ecological nature have been carried out in the general vicinity of this study. The first is that of Woodbury (1933) in Zion Canyon, Washington County, Utah. This author goes to considerable length to define and outline ecological terminology, much after the system proposed by Weaver and Clements, and has applied these terms in part to the communities found in that area. However, the montane forests are poorly represented in his area, so that few of his findings are directly applicable to the present study.

The second study of this nature was carried out by Rasmussen on the Kaibab Plateau of northern Arizona. The results of his work were prepared in manuscript form in 1932 but did not appear in print until 1941. His studies were in many ways comparable to the writer's and will be referred to at appropriate times throughout this text.

A third bio-ecological study was that of Fautin (1941). However, this work was carried out in the northern desert shrub biome of western Utah, which is strikingly different than the montane communities and has no direct bearing on the present study.

## II. TOPOGRAPHY AND GEOLOGY

### A. LOCATION AND GENERAL TOPOGRAPHY

Mt. Timpanogos (Fig. 1), where the greater part of the Wasatch study was carried out, lies in Utah County with its highest point, located at latitude  $40^{\circ} 23' 27.2''$  and longitude  $111^{\circ} 38' 42''$ . It forms a segment of the Wasatch Range which extends in a general north-south direction through the north-central part of Utah and into the southeastern corner of Idaho. Timpanogos itself lies at a slight angle to the general direction of the range with its northern extremity somewhat to the west of a north-south axis.

Extending westward from the base of the mountain is the broad and rather level floor of Utah Valley with an average elevation of about 4300 feet; and eventually, at a distance of about six miles are the waters of Utah Lake. To the eastward, after a series of low hills, is a typical back valley known as Heber Valley. This latter valley has an average elevation of about 5,300 feet.



The northern limit of the mountain is bounded by the steep walled American Fork Canyon; while the southern extremity is marked by Provo River which flows in a deep canyon completely across the Wasatch at this point. The distance separating these two canyons is about seven miles and the main body of the mountain rests upon an area of about 60 square miles.

Mt. Timpanogos represents fairly well the Wasatch Range as a whole. The general aspect is one of great ruggedness in the higher elevations, resembling in this respect the Rockies of Canada and Colorado. There are many precipitous cliffs, steep-walled canyons, jumbled masses of rocks and glaciated cirques. On the whole the mountains rise abruptly from the valley floor, especially on the west, and high altitudes are quickly attained. About 50 miles south of Mt. Timpanogos the Wasatch ends abruptly with Mt. Nebo which is within a few feet of the height of Timpanogos itself. Northward in Utah and extending into southeastern Idaho is a spur of the Wasatch known as the Bear River Range. This spur is, on the whole, less rugged than the principal range and resembles more the Uinta Mountains in topography.

An examination of the map (Fig. 1) shows that the drainage of Mt. Timpanogos is effected by a number of small streams running in four general directions from the region of the summit of the mountain. Those of the east and north run mostly in typical U-shaped glaciated canyons (Fig. 2), while those of the south and west slopes have formed V-shaped erosional canyons. The east side is drained principally by the north fork of the Provo River, while the north slope drains by numerous small tributaries into the American Fork River. Run-off from the west and south sides are carried by a number of streams, the larger of which are Grove Creek and Battle Creek.

#### B. GEOLOGICAL HISTORY

The ruggedness of Mt. Timpanogos and the greater part of the Wasatch is accounted for in its geological history. The descriptions here given are summarized from the works of Enmons (Reported by King, 1878), Gilbert (1928) and Schneider (1930).

It is generally thought that the topography of the Wasatch area, previous to the uplift of the mountains, had been reduced to a condition of low relief (peneplain). The range itself was lifted up in the form of a great block during two or three periods of faulting. The most westernly of these fault lines, commonly called the "Wasatch Fault," was the first to occur, elevating the old peneplain and tilting

its beds toward the east. Afterward, a second fault in the vicinity of Mt. Timpanogos, parallel to the first, but a few miles farther east, resulted in the formation of a second escarpment which raised the main body of the mountain to its present height. Another fault still further eastward completed the formation of the block and brought the strata to a nearly horizontal position again.

The net effect of these upheavals was to produce of Mt. Timpanogos a rugged central core, flanked on the west, north and east by a broad shoulder, shelf, or step, with an elevation of from 6,000 to 8,500 feet. On the west, this broad shoulder extends for a distance of about two miles and then drops off abruptly to the valley floor. The general evenness of its contour is marred by three principal V-shaped canyons formed by Grove Creek, Battle Creek and Dry Canyons. To the eastward the shoulder slopes off more gradually through a series of rolling hills to Heber Valley.

The relatively gentle contours of these broad shoulders, representing as it were an elevated portion of the ancient peneplain contrast remarkably with the rugged and precipitous central portion of the mountain, and these conditions effect profoundly the biota of this area.

The maximum elevation given for Mt. Timpanogos on the King-Powell topographic map is 11,957 feet. This is the only record in the files of the U. S. Geological Survey, although the height given on many road maps is 12,008.

Strata forming Mt. Timpanogos are nearly horizontal in position. They are composed of Mississippian limestones with some mixture of shales and quartzites near the summit (Gilbert, 1928, Loughlin, 1913, and King, 1878).

The geology and topography of the Uinta Mountains has been summarized by Graham (1937) based on the work of King (1878), Atwood (1989), Forrester (1937) and others, and will not be considered in detail here. However, attention should be called to certain salient factors that show contrast to the situation on Mt. Timpanogos and the greater part of the Wasatch in general and have considerable bearing upon the biotic communities of the two areas.

1. The Uinta Mountains consist of a great antecline with an east-west rather than a north-south axis such as is common to most American mountain ranges. The net effect of the antecline is to produce a high plateau with an average elevation of 10,000 to 11,000 feet and a width of thirty or forty miles. This is in contrast with the width of the Wasatch at Mt. Timpanogos which does not exceed 10 miles. Extending above this plateau are the alpine summits of the high peaks.



reaching a maximum elevation at King's Peak of 13,498 feet. In contrast to the condition over the greater part of the Wasatch, this extensive and high plateau, of the Uintas presents a relatively smooth physiognomy, making possible the development of vast climax coniferous forests upon moraines and in the basins. Furthermore, the effects of Pleistocene glaciation are abundantly evident in the form of hundreds of lakes and ponds in all stages of development.

2. The rock substratum in the Uinta Mountains contrasts remarkably with that of Mt. Timpanogos and seems to effect indirectly some of the subdominant plants. Whereas the bulk of Mt. Timpanogos is of limestone, the upper portions of the Uintas are of pre-Cambrian quartzites. This condition, coupled with poorer drainage has resulted in a general acid condition of the soil and water in the Uintas. Soils of the Timpanogos region, on the other hand, are practically neutral. pH readings supplied for me by Dr. Thomas L. Martin of Brigham Young University were as follows:

Lower Montane Climax (Timpanogos)	6.9
Aspen Subclimax (Mt. Timpanogos)	6.8
Chaparral (Mt. Timpanogos)	6.7
Upper Montane Forest (Mt. Timpanogos)	6.6
Upper Montane Climax (Uinta Mts.)	5.8

The absence of such acid tolerant plants as *Sphagnum*, *Vaccinium*, *Kalmia*, and *Ledum* on Mt. Timpanogos and their presence in the Uintas is probably accounted for in these soil differences.

### C. GLACIATION

Another force of considerable importance in the past in the two mountain areas was the extensive glaciation of Pleistocene times. This phenomenon has been described in detail by Atwood (1909). The most important effect of this glaciation on Mt. Timpanogos was the formation of three large hanging basins or cirques at elevations ranging from about 10,000 to 11,000 feet. These basins have permitted the catchment of considerable soil, so that climax alpine meadows have been able to develop under conditions of relative stability.

Glaciation in the Uinta Mountains has assisted in a general leveling of the high plateau and the formation of an abundance of small ponds and lakes and numerous moraines.

## III. CLIMATE

### A. GENERAL CLIMATE OF THE WASATCH MOUNTAINS

Climatic data for mountains, particularly the higher elevations, are



generally limited due to the fact that most of the U. S. Weather Bureau stations are located in the valleys. Most studies of mountain climates that are available are of short duration.

The most comprehensive work on the climate of the Wasatch Mountains is that of Sampson (1918) and Price and Evans (1937) at various elevations in the vicinity of the Great Basin Range Experiment Station near Ephraim. This area is about 70 miles south in a straight line from Timpanogos. Another study of relative precipitation in valleys and mountains was carried out by Clyde (1931) in the Wasatch of northern Utah. These data are perhaps the most nearly applicable to the areas considered here.

Findings of Price and Evans were based upon a 20 year period from 1914 to 1934. Data pertaining to precipitation, relative humidity, and soil and air temperatures are available from their studies. Their stations in the oakbrush, aspen-fir and spruce-fir zones correspond in general with the writer's chaparral ecotone, lower montane forest, and upper montane forest respectively. No data are available for the alpine meadow from their studies.

With regard to precipitation, Price and Evans found that the oakbrush zone (chaparral) had a mean annual precipitation of 17.5 inches, the aspen-fir (lower montane) 29.48 inches, or an increase of about 10 inches per thousand feet of elevation. The spruce-fir (upper montane) had 28.61 inches, or a decrease of 1.2 below the aspen-fir per thousand feet. Thus the maximum precipitation appears to fall in the mid-elevations. Mean annual temperatures for the various zones are given as 42.6 degrees F. in the oakbrush, 38 in the aspen-fir, and 32.5 in the spruce-fir. This amounts to a decrease in annual mean temperatures of 3.2 degrees per thousand feet of elevation. During the summer months the average decrease in temperatures per thousand feet of increase in elevation was as follows:

	June	July	August
In maxima	5.0	4.6	4.6
In minima	1.7	1.6	1.5
In mean	3.4	3.1	3.0

Thus the summer mean decrease per thousand feet is approximately the same as that for the entire year.

Shreve (1915, p. 200) found that in the Santa Catalina Mountains of Arizona the decrease in mean annual temperatures per thousand feet of elevation was 3.46 degrees F., and states that the same condition prevails on Pike's Peak, Colorado. The similarities of these figures for three rather widely scattered localities would indicate that it is

fairly safe to calculate changes from known stations on the basis of 3 to 3.5 degrees per thousand feet.

The writer's own temperature data are so fragmentary that they are of little use from a comparative standpoint, but tend in most cases to agree with this viewpoint mentioned above.

Price and Evans (op. cit.) record relative humidities for the months of May to October inclusive for the aspen-fir (lower montane) zone. The average 8 A. M. readings were as follows: May, 59.4, June, 44.6, July, 53.4, August, 54.7, September, 53.7, October, 56.1. These figures correspond with precipitation records which indicate June and September as the driest months.

Clyde (1931, p. 113) points out that winter precipitation in Utah depends upon low pressures which move eastward from northern California, Oregon and Washington and states that: "The distance these cyclonic storm paths are deflected southward largely determines the weather and amount of precipitation that falls in Utah during the winter months. The summer precipitation in Utah results principally from local storms. The warm air on hot summer afternoons upon striking the high mountains is forced to rise. As the air rises it expands and cools rapidly causing condensation and precipitation. This type of storm explains the spotted character of the intense summer storms so common in Utah."

## B. CLIMATE OF MT. TIMPANOGOS AND UINTAS

### 1. TEMPERATURE

Aside from the writer's own fragmentary records there are no available data for temperature in the stations here considered. Records have been taken for many years at Park City, Summit County about 27 miles northeast of Aspen Grove, Mt. Timpanogos. This town has an elevation of about 7,100 feet or about 200 feet above that of Aspen Grove. With this slight correction it is here taken as a standard for Aspen Grove and temperatures for other stations on Mt. Timpanogos are calculated from this standard on the basis of the findings of Price and Evans discussed above. Assuming these to be near correct, the annual mean temperatures as calculated for the writer's own station are somewhat higher than those given by Price and Evans for the same vegetational belts in their study. However, these discrepancies may be accounted for on the basis of slope, moisture and a number of other factors other than temperature that help control the altitudinal limits of vegetation.

From the writer's own records the mean temperatures of stations

in the upper montane forests of Mt. Timpanogos and the Uinta Mountains at about the same elevations are similar, but there is a considerable variance in the minimum and a lesser variance in the maximum. However, there is as yet not sufficient evidence to prove that this condition prevails continuously in the two stations. During the stormy periods in summer, in the Uintas the maxima and minima come closer together due largely to a drop in the maximum, but partly because of a rise in minimum. Following the storm the maximum rises and the minimum drops.

On Mt. Timpanogos a phenomenon noted at all of the stations was that immediately following sunset there was a rather sudden drop in temperature followed by a slight rise of two or three degrees. This rise may be due to the effect of a warm, up-canyon breeze that brings heat from the valleys early in the evening. No such situation was noted at station 3 in the Uintas.

During fair weather the minimum temperature falls at about sunrise the maximum at about 2 P. M. in the summer. At this season the mean for the day occurs at about 8 P. M.

The ability of the earth to absorb heat in the daytime and radiate it during the night is a most important factor particularly on south and west slopes of steep mountains such as Timpanogos. This probably accounts in part at least for the higher elevations of respective communities on such slopes. Following hot days these slopes radiate heat throughout the entire night. The writer has been on these areas a number of times at daybreak when it was possible to distinctly feel this radiation.

## 2. PRECIPITATION

The question of precipitation as it applies generally to mountains has been already considered in the light of the work of Price and Evans. The amount of precipitation is extremely variable from year to year and season to season. Examination of data for the American Fork Ranger station on Mt. Timpanogos showing records for ten or twelve years indicates ranges from 0.01 inches to 2.80 in June, 0.40 to 3.00 in July, and a trace to 2.99 in August. Records of snowfall and water content of the snow show a great variance also.

On Mt. Timpanogos and the Uintas the greatest part of the total precipitation occurs in late summer, winter, and early spring. The peak is generally in January and February. June is usually a dry month, but in July the summer thunder storms begin and continue into early September. In normal years these showers occur nearly every

afternoon on some part of the mountain. The summer of 1940 was unusual in that these showers did not appear, except at rare intervals, until about the first of September.

At the higher elevations the first snowstorms occur late in September or early in October, but the ground usually does not become completely or permanently covered until November. The length of time that the snow persists depends, of course, upon altitude, exposure, and the depth to which it has accumulated. On the west side of Timpanogos the chaparral community is seldom covered with snow for more than a few days at a time, and then with only a few inches. This fact is of great importance to the wintering mammals and birds in the area; especially to those birds that seek food on the ground. On the other hand, snow persists in a few places throughout the entire summer on the high cirques of Timpanogos where the ground is shaded by high cliffs during a large part of the day. On July 4, 1937 following a wet year, about a third of the ground on the Timpanogos cirque was covered with snow; at the same time in 1940 only a few snowbanks persisted. Again in 1941 a repetition of the condition in 1937 occurred. Under such conditions of wide variance in winter snow accumulated, development of vegetation in spring and early summer also varies as much as three or four weeks from year to year.

### 3. RELATIVE HUMIDITY

Relative humidity records were kept for stated times by means of a sling psychrometer during the summer of 1940. Since no hygrometers were available for continuous records the maximum and minimum daily humidities are not available. These data indicate that of the three periods of the day at which the humidity was recorded, it was generally highest at 8 A. M., lowest at noon and intermediate in the evening. The only exception was found in the aspen forest at station 2 where the humidity was higher in the evening than in the morning. This is possibly accounted for by the higher transpiration in the aspens, which, accompanied by lowering evening temperatures, brings the humidity up. By morning, part of this has precipitated as dew. This condition, however, did not prevail so markedly in August when mid-day humidity was very low due to a long drought.

A comparison of the humidity in the climax Lower Montane Forest and in the chaparral immediately across the canyon is of some interest. It will be noted that in June the relative humidity in the chaparral was considerably higher than in the conifers. This is probably correlated with the large deciduous leaf surface subject to transpiration in the



chaparral. In July the humidity at both stations was higher but the coniferous forest showed a slight increase over the chaparral. Due to the prolonged drought the herbs and lower shrubs of the chaparral had largely dried up and the increased age of the leaves of the large shrubs may have effected the total transpiration in the community.

Humidity readings taken at station 4 (9,800 feet) and station 1 (6,800 feet) within an hour of the same time in mid-afternoon showed a rise of about 5% at the higher elevation. Readings taken in June at station 3 (Upper Montane of Uintas) and station 4 (Upper Montane of Timpanogos) at the same elevations and under similar general weather conditions, show about 20% higher humidity in the Uintas. Readings taken at other times could not be compared because of different general weather conditions.

#### 4. WIND

No instruments were available for the measurement of wind velocity so that only general observations are available. In the Mt. Timpanogos region the prevailing winds are from the west. In winter they blow snow over the crest of the mountain into the high cirques where it is piled to a depth of many feet. This accumulation, coupled with the fact that high cliffs protect it from the sun, effects the climate to such an extent that trees are unable to grow and alpine conditions are established a thousand feet below their normal altitudes. To what extent these winter winds prevail in the Uinta region is not known. In summer in the Uintas, high winds are not at all common. The general condition in all kinds of weather is light breezes in the daytime and no wind at night. On the high Timpanogos cirques, however, there are nearly always high winds in the morning and these often continue throughout the day.

In addition to the prevailing winds mentioned above, there are evident, on Mt. Timpanogos, the morning down-canyon and evening up-canyon winds characteristic of the Wasatch Mountains in general. The influence of such winds may be to modify especially the minimum temperatures in summer.

#### 5. GENERAL DISCUSSION

It is evident that the climatic data for mountains and more especially for the region here considered, are far too fragmentary to permit their general application to the problems of animal distribution and habits. Only insofar as plants indicate the general nature of the climate is it possible to make such correlations. The discovery of the



exact climatic factors that influence animals depends first upon a knowledge of many climatic factors that actually prevail, and second upon experimental determination as to which of these factors apply to the problem at hand. This, of course, has not been possible in the present study.

The direct application to the community of the climatic data, as it is measured by the instruments commonly employed, is not always possible. For example, it is known that precipitation is generally greater at higher than at lower elevations which would suggest more xeric conditions at lower elevations. As a matter of fact, conditions at upper elevations are quite xeric, since the moisture is mostly in an inaccessible form during 8 to 10 months of the year. The same amount of moisture, therefore, in a warmer climate would result in an entirely different growing condition for the plants.

#### IV. CONCEPTS OF BIOTIC COMMUNITIES

In the arrangement and classification of the communities herein considered, the principles and terminology of Clements (Weaver and Clements, 1938) and of Clements and Shelford (1939) have been largely employed, with such minor modifications as have seemed necessary in the light of the findings of this investigation.

Botanists in classifying the plant communities in mountains, while all recognizing the same obvious conditions, have used a great variety of terminology in their descriptions. Graham (1937, pp. 40-43 and table 4) has summarized and compared these various systems in his treatment of the flora of the Uinta Mountains. Twelve different plans by as many authors are recorded by him.

Classification of animal communities in mountains and over North America as a whole has been no less confusing. Merriam (1892) has pointed out that up to 1891, thirty-one different zoologists had proposed systems for the division of North America into faunal regions. These were based upon distribution of different groups of animals including insects, mollusks, birds, reptiles and mammals.

The best known work on zoogeography is that of Sclater who established in 1857 six primary divisions of the world based on the distribution of the families and genera of birds. His plan was later greatly expanded and popularized by Wallace (1876). The so-called Neartic Region, composing the greater part of North America was divided into four subregions; namely, the Californian, Rocky Mountain, Alleghanian, and Canadian. These subregions correspond very little to our present knowledge of community distribution, and have

practically no application, therefore, in modern ecological work. They were not primarily concerned with the great vegetative units of the continent and cannot be considered as bio-ecological or bio-geographical. For example, the boundary between the Rocky Mountain and Alleghanian subregions almost exactly bisects the North American grasslands which Clements and Shelford (1939) have shown constitutes one of the most unique and natural biotic units on the continent. Furthermore, no recognition is given of the distinctiveness of the northern coniferous forests and the arctic tundra. Little consideration was given to mountain faunas. These faults, as well as a number of others, have been pointed out long ago by Merriam (1892), Allen (1892) and possibly other workers.

The most widely used system of community classification in North America, particularly by zoologists, is the Life Zone system proposed by C. Hart Merriam in 1894 and 1898. Since this system has been widely used in the study of mountain communities and has perhaps found its best application there, it deserves some discussion at this point.

Merriam's life zone concept was really conceived in connection with his study of San Francisco Mountain in Arizona (1890) but was later extended to include the whole of North America. As has been pointed out by Daubenmire (1938, p. 330), the original classification of North American biotic communities as indicated in his early map of "Life Areas" was a more nearly correct representation of the biotic communities as they are now known than his later map which was based upon temperature and has been more widely used. This classification of zones, as indicated in Merriam's study of San Francisco Mountain, was based upon biogeographical factors, although named from areas rather than from dominant plant formations. Furthermore, Merriam recognizes to a degree the climatic control of his major communities, designating temperature and humidity as of paramount importance, especially insofar as the growing season is concerned.

As is well known, Merriam later emphasized temperature as the all important factor in animal and plant distribution. These life zones, applied to the whole of North America, were based upon the sum of positive temperatures, supposedly above 6 degrees C. for the season of growth and reproduction for northward distribution. He regarded the mean temperature during the hottest part of the summer as the governing factor in southward distribution. As has been pointed out by Shelford (1932a, p. 147) his temperature data were supplied by the Weather Bureau, and the sums were calculated above 0 degrees rather

than above 6 degrees and the error was never corrected on the maps.

The life zone concept has been used widely in studies in western mountains (Cary, 1911, 1917), but the zones are invariably based upon indicators rather than upon specific features of temperature. This is due to the fact that temperature data are not generally available for mountains, and the dominant vegetation gives the best index to the total climate. An indication of this viewpoint is given by Hall and Grinnell (1919, p. 38) in the following quotation:

"The idea that life zones are altitudinal or latitudinal is correct only in a very general way or incidentally. They are, instead, primary biologic, that is, they are composed of and determined by a certain assemblage of plant and animal species, and are effected by altitude only as they modify the climate, more especially the temperature during the critical periods of an organism's existence."

In numerous biotic studies of mountains in the west the life zone system or some modification of it has been used. Typical examples are Merriam's study of San Francisco Mountain (1890) and Mt. Shasta (1899), Carey's work in Colorado (1911) and Wyoming (1917), the work of Grinnell and others (1930) on Lassen Peak, California, and of Taylor (1922) on Mt. Rainier, Washington.

The life zone system has never found favor with most botanists chiefly because it did not take into account all of the climatic factors that effect plant distribution, and because the limits of the boundaries based on isotherms do not coincide with the actual distribution of plants. In addition, this concept has been criticized on a number of grounds by several zoologists (Allee, 1926, Kendeigh, 1932, Shelford, 1932, and others). No attempt will be made to repeat these criticisms here.

The writer feels that the life zone system is inadequate in the present study for the following reasons:

1. The life zone system does not ordinarily take into account the dynamic bio-ecological factors of succession, aspection, annuation, and interaction which are so vital to the understanding of biotic communities.

2. Although, as interpreted by many who have followed in the footsteps of Merriam, the life zones do represent the major biotic communities as found in mountains, they are not applicable continentally and tend, therefore, to confuse rather than to help in the stability of terminology as applied to larger areas.

3. The older term "formation" as expanded by modern ecologists to include animals (biotic formation or biome) not only has priority in usage (Grisebach, 1838) but as now used meets most of the objections indicated above.

Dice (1922, 1938, 1939) has divided parts of North America into biotic areas or "biotic provinces," based largely upon the distribution of plants, mammals and reptiles. However, it can at once be seen by comparing his maps with that of Weaver and Clements (1938) that his Canadian Province coincides generally with the Lake Forest (Pinus-Tsuga Formation) now thought by some to be an ecotone (Pitelka, 1949); his Sonoran Province has almost exactly the same limits as Clement's Desert Shrub (Larrea-Fraseria Formation).

Still more recently (1943), Dice has expanded his system of biotic provinces to include the whole of North America. These provinces are further subdivided by him into biotic districts and life belts. However, this writer proposes his system only in a tentative way, and there appears to be insufficient data, especially insofar as the region under study is concerned, to make it applicable at the present time.<sup>(3)</sup>

Davis (1939) in his "Mammals of Idaho," has used the term "biotic area" in designating the vegetational and faunal areas of that State. He also mentions the usage of this term by Clark in 1937, and apparently overlooked its still earlier use by Dice (1922). In 1892 Allen used the term "life area" which means about the same. While Davis' treatment may have certain advantages, it cannot be used in an ecological sense since it is purely bio-geographical and does not undertake to include succession and the other dynamic ecological factors. Furthermore, the term "association" as used by him to include both developing and climax communities is not in accord with its usage by many plant ecologists.

The development of the bio-ecological concept which is used in this study, has been reviewed by Clements and Shelford (1939, pp. 1-19) and by Carpenter (1939, pp. 75-89). It will, therefore, not be necessary to consider it in detail here. It treats both land and water communities, but it is used here, of course, only in connection with land. This concept has long been recognized, especially for water, but has been advanced especially in recent years by Clements (1905, etc.), Shelford (1907, etc.) and by a number of the latter's students. Phillips (1931) in South Africa and Kashkarov (1938) in Russia have similar points of view.

It is sufficient to say here that the bio-ecological concept meets the greater part of the requirements for the modern worker in community studies. It treats of the communities as biotic entities designating them primarily on the basis of life forms of their dominant organisms, and taking into account the influence of the animals. Furthermore it deals

(3) Op. cit.



with the dynamics of the communities, taking into consideration their development, populations, aspections, annuations and all the interactions that give character and continuity to the communities as a whole.

## V. THE MONTANE FOREST

### A. LOWER MONTANE FOREST

(Figs. 1-4 and Table I)

#### 1. CLIMAX FOREST

The climax stage of the Lower Montane Forest may be technically designated as the *Pinus ponderosa*-*Pseudotsuga mucronata*-*Abies concolor* Association (Yellow Pine-Douglas Fir-White Fir Association). It is characterized and separated from the Upper Montane principally on the basis of its dominant plants which are an expression of climatic differences. On its lower border this community comes in contact with the chaparral ecotone of the foothills which is to be described in a later paper, (Figs. 1 and 2). There is no mammal confined to it or particularly characteristic. The red-breasted nuthatch is apparently confined to it in the region studied but studies in other areas do not bear out the universal application of this observation.

On Mt. Timpanogos the Douglas fir (*Pseudotsuga mucronata*) and white fir (*Abies concolor*) form the dominants (Fig. 2), while in the Uinta Mountains the Yellow Pine (*Pinus ponderosa*) enters into the picture. This pine is absent from Timpanogos. Where present the yellow pine forms an open type of forest and occupies the lower and more xeric portions of the association. Some question arises as to the role of the white fir in this association. The porcupine feeds extensively on this tree in winter, while it seldom, if ever, attacks the Douglas fir. In some places it appears that the white fir is being gradually destroyed by this coation in which case the Douglas fir should ultimately form a consociation. In the northern Wasatch the white fir is entirely absent.

Station 1 of this study is located in perhaps the most extensive and best preserved Lower Montane association on Mt. Timpanogos, (Fig. 2). This community is represented only as small patches which invariably occur on north- or east-facing slopes of canyons. There is no continuous and unbroken forest over the entire areas; and this condition generally holds throughout the Wasatch Mountains. It is also true that some of the trees have been removed by man, causing a more open canopy and thereby modifying somewhat the vegetation of the forest floor.





Fig. 2. Portion of east face of Mt. Timpanogos in vicinity of Aspen Grove. A, Area of final aspen replacement by conifers. B, Snowslide path through conifers. C, Lower Montane climax and seral stages. D, Upper Montane subclimax. E, Chaparral ecotone.

TABLE 1

Summer populations of various groups of invertebrates taken in quantitative samples during 1939, 1940, and 1941. Numbers are averages of all 48 sweep samples taken. Percentages are in round numbers and represent per cent of the total invertebrate population.

	Lower Montane Climax								Aspen Subclimax								Upper Montane Climax						Upper Montane Subclimax								
	Gr.*		Herb		Shrub		Tree		Gr.*		Herb		Shrub		Tree		Gr.*		Herb		Tree		Gr.*		Herb		Shrub		Tree		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Diplopoda	2.0	4.0							4.0	0.3																					
Chilopoda	10.0	20.0							12.0	9.0																					
Araneida	4.0	8.0	3.0	7.0	5.0	12.0	9.0	37.0	16.0	12.0	**	0.9	5.0	4.0			8.0	44.0	**	2.0	2.0	13.0			1.0	0.7		1.0	1.0		
Acarina	4.0	8.0							12.0	9.0							6.0	33.0						4.0	25.0						
Mollusca									2.0	0.2																					
Formicidae	26.0	52.0	2.0	4.0	4.0	10.0	**	0.8	16.0	12.0	2.0	3.0	1.0	2.0	4.0	4.0		1.0	6.0	**	4.0			2.0	12.0	3.0	2.0	3.0	6.0		
Par. Hymenoptera			2.0	4.0	3.0	8.0	1.0	4.0			4.0	6.0	3.0	5.0	2.0	2.0		2.0	12.0	2.0	13.0				4.0	3.0	2.0	5.0	5.0	6.0	
Other Hymenoptera							**	1.0			**	0.3	**	0.5	**	0.2				**	0.8				1.0	0.7	**	1.0	1.0	1.0	
Staphylinidae	2.0	4.0							26.0	20.0														2.0	12.0						
Carabidae									18.0	14.0							2.0	11.0													
Other Coleoptera			2.0	4.0	4.0	10.0	**	0.8	2.0	0.2	2.0	3.0	1.0	2.0	**	0.2				**	4.0				2.0	1.4	2.0	4.0	3.0	3.0	
Hemiptera			1.0	2.0	1.0	2.5	1.0	4.0	2.0	0.2	11.0	15.0	4.0	7.0	3.0	3.0	2.0	11.0	**	1.0	**	8.0			15.0	10.0	5.0	10.0	1.0	1.0	
Cicadellidae			28.0	61.0	6.0	16.0	1.0	4.0			38.0	53.0	21.0	34.0	87.0	87.0		5.0	30.0	**	2.0				73.0	53.0	30.0	60.0	52.0	62.0	
Aphidae			4.0	8.0	9.0	22.0	**	0.8			4.0	6.0	16.0	25.0	**	0.4		1.0	6.0	**	2.0				30.0	20.0					
Other Homoptera			**	1.0														**	3.0	**	2.0								8.0	10.0	
Diptera			4.0	8.0	7.0	17.0	13.0	50.0			10.0	13.0	12.0	20.0	6.0	6.0		7.0	41.0	9.0	60.0				9.0	7.0	3.0	6.0	13.0	15.0	
Arthropoda																									1.0	0.7					
Insect larvae	6.0	12.0			1.0	2.5	1.0	4.0	19.0	14.0		**	0.5	2.0	2.0				**	0.8				8.0	50.0	1.0	0.7	3.0	6.0		

\* Samples taken in the open and not under the protection of logs, rocks, etc. One square meter.

\*\* Less than one.



## a. GROUND LAYER SOCIETY

Since the Lower Montane climax usually occurs on steep hillsides, the soil is very shallow (a foot or less in depth), and well drained. The upper two to six inches is composed of conifer leaves and other organic matter in various states of decay. This layer may become quite dry in summer. Many fallen and partly decayed logs are in evidence.

The reaction of dominants and subdominants is therefore of considerable importance. By making measurements in typical situations the writer has estimated that from 10–20% of the ground is covered with fallen logs, stumps and larger branches in various stages of decay. It is under and in such places that much of the animal life of the ground layer is to be found.

Certain animals also react rather importantly upon the ground layer. Midden piles of the red squirrel (*Tamiasciurus hudsonicus ventorum*) are the most important. These piles consist of cores and scales of cones, the seeds of which have been utilized as food, as well as a considerable number of stored cones that have not been removed. The piles are generally perforated with holes in which the cones are stored. Midden piles cover areas of from 8 to 15 square meters and may have a depth of 36 centimeters or more.

Nearly all of the common invertebrates of the ground layer inhabit these midden piles.

Scats of deer, porcupine, snowshoe rabbits and squirrels add somewhat to the content of the soil. Those of the snowshoe rabbit are most generally distributed and conspicuous on the soil surface. An average of 10 per square meter was found over the entire area at one time.

The reaction of burrowing animals on the ground layer is not an important factor in the Lower Montane association, except for the activity of the red squirrel in the midden piles. Gophers enter the climax very little and ground squirrels only to a limited extent. An average of 12 summer gopher diggings and 20 ground squirrel burrows was found in 1 hectare and part of this area was not climax.

Ants, particularly of the genus *Camponotus*, play a large part in breaking down logs that are fairly well decayed. Several species of *Cerambycidae* and *Buprestidae* mine fallen logs in various stages of disintegration.

There is little plant life associated directly with the soil layer. A few mosses and lichens, also characteristic of the Upper Montane, are to be found, and fungi of many kinds grow in the litter and on the fallen logs and stumps.

Ants are the most important invertebrates in the soil layer, although

a number of the species climb up into the herb, shrub and tree layers. About 52% of the invertebrate population in open spaces is ants, but the greater concentrations are under logs and rocks where they build their nests. About 50% of the logs or rocks turned over had ant nests under them. The giant carpenter ant (*Camponotus herculeanus rhymperei*) is most frequently found nesting in well decayed logs where it usually has extensive galleries. Six other species of ants have been found in the ground layer. Ants form a large part of the food of the red-shafted flicker which is often seen tearing at the decayed logs.

Mollusks do not usually appear in samples taken in exposed places, but live almost exclusively under the protection of logs and rocks. Furthermore they fluctuate in numbers a good deal depending upon the amount of precipitation. During the summer of 1940 when there was little rain from June to September, mollusks disappeared almost entirely. In the summer of 1941, however, following a winter of heavy snow and consistent summer rains, mollusks were in evidence throughout the season. They were abundant under logs and occasionally appeared in samples in open areas. *Vitrina alaskana* is the most common mollusk of the community, comprising about 75% of the population of snails. Six other species of lesser abundance are also known to occur here.

Two species each of centipedes and millipeds have been found in exposed places and together form about 24% of the average invertebrate population. Three species of spiders, making up 8% of the population, have been found and there are a number of mites as yet undetermined. Insect larvae of beetles and Diptera occur to the extent of about 12% of the average population. Beetles are present in the ground layer but not common. The northern ground beetle (*Pterostichus protractus*) is found mostly under logs and rocks, but is often seen moving about over the surface of the ground at night. There are from 1 to 5 of these beetles under nearly every log turned over. Several species of the staphylinid subfamily Aleocharinae were found but as yet are undetermined.

#### b. LOW SHRUB-HERB LAYER SOCIETY

A mixture of low shrubs and herbs, difficult to separate in the quantitative samples, are here considered together in this layer. The principal shrubs are *Pachistima myrsinites* and the Oregon grape (*Odostemon repens*). Some of the more common herbs are: *Polemonium albiflorum*, *Sophia leptostylis*, *Mitella stenopetala*, *Arnica cordifolia*, *Viola montanensis*, *Thalictrum fendleri*, *Smilacina sessili-*



*folia*, *Smilacina amplexicaulis*, *Fragaria bracteata*, and *Galium triflorum*.

The density of the vegetation in this society depends upon the amount of shade. In places where the tree canopy is very dense there is practically no undergrowth, but in areas where an opening permits some direct sunlight the growth may be very luxuriant.

About 32 identified species of invertebrates are known to inhabit this community. These include 7 species of spiders, 4 of beetles, 2 of Hemiptera, 3 of Diptera, 7 of leafhoppers, 3 of aphids, 3 of ants and at least 4 species of parasitic Hymenoptera.

Leafhoppers comprise about 61% of the average invertebrate population. These are made up mostly of a small pale brown species, *Dikraneura carneola*, which is very common throughout the mountains, and a small green species of the *Empoasca fabae* group. These leafhoppers are present from May to September, but August and September populations show an increase of about 4 times that of June and July. This may be associated with vegetation growth, since the herbs ordinarily do not become well grown until the middle of July.

#### c. TALL SHRUB SOCIETY

The tall shrub society consists mainly of two species, the ninebark (*Physocarpus malvaceus*) and the mountain ash (*Sorbus scopulina*). Ninebark is a shrub of medium height, averaging 4 feet; while the ash is taller, often reaching a height of 8 or 10 feet. There are also a number of other shrubs in the layer including the serviceberry (*Amelanchier alnifolia*), mountain willow (*Salix scouleriana*), mountain maple (*Acer glabrum*), chokecherry (*Prunus melanocarpa*), thimbleberry (*Rubus parviflorus*), and bitter buffaloberry (*Lepargyrea canadensis*).

About 9 species of spiders have been found on the shrub layer. Many specimens could be determined only to genus so that it was difficult to trace the seasonal occurrences. *Theridion placens* and *Paraphidippus marginatus* appeared the most times in samples and in the greatest numbers. Spiders formed an average of 12% of the invertebrate population.

Two species of weevils, *Thricolepis inornata* and *Dyslobus wasatchensis* Tanner, are very common on ninebark and other shrubs from about the middle of June to the first of July. During that time they comprise about 40% of the invertebrate population. Details of their life histories are not known but *Thricolepis* feeds on the leaves of the chokecherry, ninebark and other shrubs, while *Dyslobus* seems to be confined mostly to ninebark.

Eight species of Diptera were identified from the shrub layer. Two biting flies *Symphoromyia fulvipes* and *Chrysops noctifer* were especially abundant from about June 15 to July 15 in 1940. In 1941 they did not appear until July 1 and remained until about August 15. They seem to use shrubs, and to a lesser degree herbs, as resting places. Deer seem to be annoyed considerably by these flies. This may partly account for the seeming tendency for the deer to move into the Upper Montane in mid-summer, since these flies are not nearly so abundant there.

Aphids formed an average of about 20% of the invertebrate population on shrubs. *Myzus monardae* was the most abundant species. Leafhoppers of 4 species comprised about 16% of the population.

Populations of all the invertebrates of the shrub layer except leafhoppers was highest in June and July and dropped off in August and September. This may have been due in part to a drying up of the leaves during late summer; however, the chief cause was the browsing of some sheep in the area during the latter part of the season.

#### d. THE TREE LAYER SOCIETY

The tree layer is formed by the canopy of the Douglas fir (*Pseudotsuga mucronata*) and the white fir (*Abies concolor*). Since only two or rarely three species of plants are involved it presents a somewhat monotonous habitat, and the animals are relatively fewer in number as well as in species represented.

A characteristic of this layer is a large proportionate number of spiders. The Araneida here form about 37% of the invertebrate population. This seems to distinguish the Lower from the Upper Montane, since the latter possesses a much lower population especially in the subclimax type found on Timpanogos. At least 7 species of spiders were found in the tree layer, but many of the young specimens could not be determined beyond the genus. Those species found most often in the samples were *Aranea displicata* and *Philodromus pacificus*.

Another feature of the tree layer is the large number of Diptera that are constantly seen flying about in open spaces in the canopy in sunny weather. These flies are mainly Syrphidae of the following species: *Metasyrphus luniger*, *Metasyrphus lapponicus*, and *Syrphus opinator*. These flies use the trees as resting places between flights. They are an important source of food of Hammond's flycatcher. A considerable number of flies of the family Anthomyiidae appeared in the samples in July, but were not found at other periods.

Leafhoppers were far less abundant than on the herb and shrub

layers. Ants, beetles, insect larvae, Hemiptera, and parasitic Hymenoptera appeared in minor numbers.

Most of the invertebrate animals occurred in such small numbers that it was difficult to detect any population changes in summer. Ant populations of the soil remained about the same throughout the summer. Leafhoppers showed a definite tendency to increase gradually from June to September in the two layers where they were abundant. Spiders in the tree layer appeared to reach their greatest abundance in July and to drop off markedly in August and September. This may be due to migration into the herb and shrub layers during this period, since there seems to be an increase here in spiders of the same species. At least four species have been found in both layers.

## 2. ASPEN SUBCLIMAX

The greater part of the Lower Montane Forest of Mt. Timpanogos occurs in the form of a subclimax forest of aspen which may be technically known as the *Populus tremuloides* Associates (Aspen Associates). The aspen is capable of growing through a considerable range of altitude and in a variety of habitats and assumes a somewhat different form depending upon local conditions. On steep hillsides where soil is shallow and pressure of snow against the trunks is great, the trees are scrubby and distorted and present few characteristics of a mature forest. In areas subject to snowslides the trees occur in groves of different heights depending upon how recently they were swept away by the snow. These snowslides effect large areas in the Timpanogos region, so that there are many places where the aspens are kept in a perpetual state of immaturity and never gain such proportions that they may be called trees.

The older and best developed aspen forests occur on the flattened benchlands of the north and west shoulder of the mountain where the soil is deep and rich, moisture content is comparatively higher, and there are none of the devastating effects of snowslides. In other sections of the Wasatch they are found under similar conditions of stability. The altitude range is between seven and eight thousand feet. In such areas these forests have apparently gone on for several hundreds of years, judging from the large trunks of fallen trees in various stages of decay that are to be found on the forest floor. Scattered through these forests are large specimens of white fir, showing fire scars, which may have been the remains of an old coniferous forest. Certain sheepmen who have been acquainted with the area for many years claim that a coniferous forest was swept off by fire about 70

or 80 years ago; but it seems to the writer that if such were the case there would be more evidence in the form of fire scarred stumps. It appears likely that if such a fire occurred it must have taken place several hundreds of years ago.

The principal area of study for the aspen forests was at Big Tree Camp and is referred to as station 2 (Fig. 3). It was situated in an old forest with many large living trees that frequently gain a diameter of 18 inches. There are also many other dead standing trees as well as fallen logs in various stages of decay.

#### a. GROUND LAYER SOCIES

Reactions of plants and animals are evident here as in the climax forest, but are of a somewhat different nature. Fallen logs, stumps and branches are much in evidence covering an estimated 10-20% of the ground surface. A luxuriant growth of herbs as well as aspen leaves added each autumn have built up a rich loam several feet thick. There is no thick layer of leaves on the forest floor as there is in the conifers since the aspen leaves disintegrate more rapidly, usually within a year or two, and are quickly added to the soil.

The soil turning activities of animals are here much more important than in the conifer forest. Counts show a maximum of 40 gopher diggings and 60 ground squirrel holes per hectare. Each gopher working consists of a chain of earth piles from ten to twenty feet long. Gophers are active throughout the year, and in early spring, just after the snow has gone, their winter cores that are made as they burrow in the snow often form a continuous network over the ground that may cover the entire forest. It was estimated that in many places fully a third of the soil was turned over annually in this way. The importance of this reaction to the forest floor has been described by Grinnell (1923).

The ground layer contains many of the invertebrates common to the ground layer of the coniferous forest, but they occur in greater numbers. The average population of all invertebrates in the conifer forest was about 52 per square meter while that of the aspens was 130 (Fig. 10). There were 2 species of mollusks, 2 centipedes, 2 millipedes, at least 10 species of spiders, 15 of beetles, 5 of ants, and 5 species of ground nesting social wasps identified in this study.

Ants are relatively less abundant, forming only 12% of the total populations. Beetles are relatively much more abundant and make up nearly 50% of the total population. Eight species of Carabidae have been found in this layer. (See appendix B.) *Pterostichus protractus* is the most common species found under logs. Smaller species of the





Fig. 3. Portion of east face of Mt. Timpanogos showing expanse of aspen subclimax in foreground. A, Small areas of replacement of aspen by alpine fir (*Abies lasiocarpa*). C, Lower Montane. D, Upper Montane subclimax. F, Chaparral ecotone.

coleopterous genera Bembidion, Calathus and Blechnus are usually found in samples taken in exposed areas although at least 13 species of Carabidae and Staphylinidae appeared in the quantitative samples.

Beetles along with ants are eaten extensively by the robin, red-shafted flicker, and hermit thrush all of which feed a great deal on the ground. The ruffed and dusky grouse also scratch a great deal in the soil especially in spring and early summer, before fruits are ripe. A few stomachs that the writer has been able to examine have shown parts of ground beetles in the contents.

In dry years especially, such as the summer of 1940, a number of species of paper wasps of the family Vespidae construct their nests under logs or piles of leaves and debris. The most common species are *Vespula norvegica norvegicoides*, *V. vulgaris*, *V. arenaria*, and *V. maculata*. The last named species more commonly nests in trees but occasionally builds underground. It would appear to the writer after several years of observation, that lack of beating rains, especially during midsummer, favors the survival of wasp colonies; while heavy rains tend to destroy the paper nests. This may account for their abundance in dry years. Precipitation records at the South Fork ranger station show the summer of 1928 to be extremely dry, and it is known that wasps were unusually abundant that year. They were abundant again in 1940, another dry summer, and scarce in 1941 when there were continuous summer showers. These wasps lap up honey dew secreted by aphids and prey upon leafhoppers and possibly other insects. They have many times stolen leafhoppers from tips while the writer was preserving specimens.

#### b. THE HERB LAYER SOCIES

The herb layer socies shows in many places the effects of overgrazing, which results in a growth of rank herbs that reach a height of three or four feet. The most conspicuous of these are the nigger-head (*Rudbeckia occidentalis*), tall larkspur (*Delphinium occidentale*), stickseed (*Lappula floribunda*) and tall senecio (*Senecio serra*). In certain places the common bracken (*Pteridium aquilinum pubescens*) occurs almost to the exclusion of all other plants. There are in addition about 15 other species of common forbes.

In early spring, immediately following the snow, there is a vegetational aspect composed chiefly of two early blooming species: the spring beauty (*Claytonia lanceolata*) and dog-toothed lily (*Erythronium parviflorum*).

In contrast to the condition found in the climax coniferous forest of the Lower Montane, a great many grasses are to be found in the

herb layer of the aspen forest. These grasses consist both of valley grassland forms that are able to penetrate to this altitude and species which are more characteristic of the montane and northern floras. Those species that are common to lower elevations include: *Agropyron inerme*, and *Elymus glaucus* dominants of the Palouse Prairie (Clements and Shelford, 1939, p. 291), and *Bromus carinatus*. Species that are principally montane include: *Poa pratensis*, *Poa curta*, *Agropyron subsecundum*, *Agrostis hiemalis*, *Stipa lettermani*, *Stipa columbiana*, *Stipa pinetorum*, and a common sedge, *Carex festivella*.

The herb layer supports a high population of invertebrates. At least 18 species of Diptera, 5 of Hemiptera, 9 of leafhoppers and 4 of psyllids and aphids were identified. In addition there have been found 3 species of ants and 14 of parasitic Hymenoptera of the Braconidae, Dryinidae, Ichneumonidae, and Chalcidoidea. It is probable that the dryinid *Anteon* may be parasitic on some of the leafhoppers of the community, but it has not been possible to show which species.

Leafhoppers are the most abundant insects found in this layer, comprising 38% of the invertebrate population. Diptera occur to the extent of 11%, and Hemiptera form 11%. In common with the herb layer in general in forests, very few birds visit the herbs for food, presumably because of the difficulty in lighting on the fragile plants. However, the house wren has been seen on stalks of niggerhead where it was apparently feeding on aphids and leafhoppers.

In addition to the species commonly taken in sampling, there are a number of bumble bees (Bremidae) that visit the herb layer throughout the summer. The most common species are *Bremus occidentalis*, *B. centralis*, *B. oppositus*, *B. bifarius*, and *B. rufocinctus*.

#### c. THE SHRUB LAYER SOCIES

The shrub layer is less conspicuous in the aspens than in the coniferous forest. It appears as scattered clumps rather than continuous thickets. In all cases it is far less conspicuous than the herb layer. The most common shrub, especially in the vicinity of station 2, is the red elderberry (*Sambucus microbotrys*) which stands to a height of 3 or 4 feet in many places. The snowberry (*Symphoricarpos vaccinioides*) is also frequently found especially in rocky soil. Low-growing shrubs such as *Pachystima* and *Odostemon* are found on steep slopes.

Most of the sampling for this study was done on red elderberry and snowberry. Invertebrates found here and identified include at least 13 species of Diptera, 4 of Hemiptera, 6 of leafhoppers, 3 of aphids, 3 of ants, and 7 of parasitic Hymenoptera of the Chalcidoidea, Braconidae, and Ichneumonidae.



Fig. 4. Portion of northeast shoulder of Mt. Timpanogos. A, Conifer border along cold stream. B, Large area of alpine fir (*Abies lasiocarpa*) replacing aspens. C, Montane forest, mostly aspen subelimax. F, Chaparral ecotone on west-facing slopes.



In the shrub layer, leafhoppers are again the most abundant invertebrates, forming about 34% of the total population. Diptera, including many species of Anthomyidae, are also very abundant and form about 20% of the total populations over all seasons and years that samples were taken. In this layer birds are more often seen feeding. The chipping sparrow is especially common here and gains a large part of the food for its young from the shrub layer.

#### d. THE TREE LAYER SOCIES

The aspen is the only plant dominant in the community and forms the canopy of the forest. A few conifers occur over the area but the samples were confined entirely to the aspens.

In this community there have been identified about 3 species of aphids, 5 of leafhoppers, 3 of Hemiptera, 5 of ants and a few species of parasitic Hymenoptera and beetles. Less species are represented in this layer than in the herbs and shrubs: for instance there are only half as many species in the tree layer as in the shrub layer. This is in harmony with the general monotonous condition of the habitat.

Leafhoppers are by far the most conspicuous part of the leaf fauna in general and comprise about 87% of the invertebrate population. Most of them belong to the genus *Idiocerus* of which the following species are represented: *I. formosus*, *I. suturalis*, *I. lachrymalis*. The nymphs hatch out about the time the leaves appear and can be found in various stages of development throughout the summer.

Leafhoppers are eaten extensively by a number of the birds of the aspen canopy. The warbling vireo, Audubon's warbler, and house wren are especially important in this respect.

In certain localities, particularly during the summer of 1940, the small pale green aphid *Chaitophorus populifoliae* was abundant on the leaves of the aspen causing them finally to curl up on the edges and die. These aphids excrete large quantities of honeydew which covers the aspens with a sticky film and drops down on the vegetation below. This excretion accumulates to a great extent when there are no rains to wash it away. About 5 species of ants have been found associated with these aphids, presumably feeding upon their excretion. In addition a number of predaceous insects eat the aphids. These include the lady beetle *Cyclomeda polita* and the anthocorid bugs, *Anthocoris antevolens* and *Anthocoris melanocerus*.

Almost continuous files of ants of several species may be seen throughout the day traveling up and down the aspens and on the foliage. These insects are eaten by various species of woodpeckers and sapsuckers that are found in the aspen forest, such as the hairy

woodpecker, downy woodpecker, red-naped sapsucker, and red-shafted flicker.

Certain Lepidoptera, as yet undetermined, use aspen leaves in the construction of their chrysalises. These are made either by fastening two leaves together and sealing them with silk or bending the leaf on itself until the two edges meet and then fastening them together by cross strands on the inside. The larvae also feed upon the leaves. These chrysalises are formed in early June and are found empty by mid August or sooner.

Examination of the data on season abundance shows a great deal of irregularity in many of the groups, especially the ground invertebrates. Diptera, reaching their greatest abundance in the shrub and herb layers, showed a general decline in numbers as the summer advanced. It is of interest to note that in the case of the leafhoppers there was a tendency to increase on herbs and decrease on trees as the season progressed. Birds in large numbers feeding on trees and seldom feeding on herbs may have been partly responsible for this condition. It is at least a matter that would be worth investigation. The sudden drop in leafhoppers on the shrubs in September 1940 may be associated with the dry summer and the fact that most of the leaves had dried up and fallen off by the first of September. Herbs and trees suffered less from this condition. A great increase in population in the herb layer in August may be traced to the presence at that time of large numbers of Hemiptera nymphs of the family Anthocoridae.

### 3. UINTA MOUNTAINS LOWER MONTANE FOREST

The Lower Montane as it is found in the Uinta Mountains has been described as far as the vegetation is concerned by Graham (1937, pp. 51-53, 75-77) and coincides in general with his Aspen and Lodgepole zones. It differs from the Mt. Timpanogos forest principally in the addition of two dominant trees, the lodgepole pine (*Pinus murrayana*) and the yellow pine (*Pinus ponderosa*). There are also other minor differences in vegetation.

This forest has not as yet been studied quantitatively and for this reason cannot be compared with the Timpanogos forest at this time. Such general studies of the vertebrate animals as the writer has been able to make at Soapstone and Elk Park indicate that the relationships in the two areas are about the same. Svihla (1932, p. 54) notes that the Utah jumping mouse (*Zapus princeps utahensis*) is confined to this community while (*Clethrionomys gapperi galei*, the red-backed mouse, is found only in the Upper Montane. Neither of these situ-

ations occurs on Mt. Timpanogos, for the writer has found both species ranging throughout the entire Montane Forest. However, the writer's work in the Uintas has not disproved her statement for that area.

Lists of birds from the two areas show no outstanding differences.

## B. THE UPPER MONTANE CONIFEROUS FOREST

(Fig. 5)

### 1. CLIMAX FOREST

The climax Upper Montane Forest (Fig. 5) may be known technically as the *Picea engelmanni* - *Abies lasiocarpa* Association (Engelmann Spruce-Alpine-Fir Association). This forest is well developed at higher elevations in the Uinta Mountains, and there covers extensive areas. On Mt. Timpanogos it has apparently not reached a biotic climax due to a variety of factors which will be considered later in the text.

Graham (1937, pp. 79-80) has described this forest as it is found in the Uinta Mountains. The writer's own studies were carried out principally in the west end of the range in the vicinity of Lost Lake (station 3). In this area the climax forest is composed mostly of a single dominant (*Picea engelmanni*) with *Abies lasiocarpa* of only secondary importance. The Rocky Mountain pine marten appears to be chiefly confined to climax forests and reaches its greatest abundance in the Upper Montane although it undoubtedly occurs to some extent in the Lower Montane as well.

#### a. GROUND LAYER SOCIETY

In the Upper Montane the ground is not covered with a growth of mosses and lichens as is that of the Northern Coniferous Forests of Canada. However, the foliose lichens of the genera *Peltia* and *Usnea* do occur. The latter is most often found growing on well-rotted logs. Also forming a low mat on the surface of the ground, especially in more shaded places, are a number of mosses including *Polytrichum gracile* and *Polytrichum juniperinum*. These mosses and lichens are much more conspicuous in the Upper Montane than they are in the Lower Montane.

Reactions of the organisms of the Upper Montane are in general the same as in the Lower. Fallen logs and branches are a conspicuous feature of the forest floor, covering from 10% to 30% of the ground surface. Due to the extremely shallow nature of the soil, windfalls are frequent, and bare areas resulting from uprooted trees are conspicuous features of the forest floor.

The carpet of decaying leaves is not as thick as in the Lower Montane but is nevertheless present. Midden piles of the red squirrel are not nearly so common presumably because there are more hollow trees in which to store the cones, but they do occur in scattered numbers. The Rocky Mountain hairy woodpecker and presumably the alpine three-toed woodpecker contribute somewhat to the litter of the forest floor by flipping off the scales of the bark of the Engelmann spruce. This is done as the birds search for food, and the scale piles are often conspicuous about the bases of both dead and living trees.

Since gophers and ground squirrels seldom enter these climax forests there is little burrowing activity carried on there.

The invertebrate animals of the ground are not abundant and are confined mostly to the undersides of logs and rocks. A list of the invertebrates found in this layer includes 1 species of mollusk, 4 species of spiders, 9 of beetles and 3 of ants. There are also several species of mites as yet undetermined.

Invertebrate populations in the ground are among the lowest of any of the communities studied (Fig. 10). They are much lower than those of the Lower Montane climax (18 as compared to 52 per square meter). Spiders and mites are the most numerous and together form about 77% of the invertebrates. Ants are much less abundant, there being none represented in the samples taken. Nearly all of the ants occur under the protection of logs and rocks, and even there are much less abundant than in the Lower Montane. Wheeler (1917) states that this same condition occurs in the Sierra Nevada Mountains, and that it is due to cold and more moisture, both of which together are unfavorable to ants. Myriapods, while present, are not nearly as abundant as in the Lower Montane.

Mollusks are limited both as to number and species. They are also very uncommon in ponds of the area. This absence of mollusks is probably due in part at least to the fact that the water and soil are acid, the substratum of quartzite making it difficult for them to elaborate the calcareous materials necessary for the shells.

#### b. THE HERB-LOW SHRUB SOCIETY

The undergrowth in this layer is composed of low-growing shrubs and herbs so intimately mixed together that it is difficult to separate them in quantitative collecting. There is no tall shrub layer as there is in the Lower Montane. The most conspicuous of the shrubs are two species of blueberry (*Vaccinium oreophilum* and *V. scoparium*). These often form a dense mat 4 to 6 inches high. Another shrub, slightly taller, is the red gooseberry (*Ribes montigenum*) which usu-



ally grows next to the trunks of trees. Some of the more conspicuous herbs of this community include *Pedicularis racemosa*, *Thlaspi glaucum*, *Erigeron salsuginosus*, *Juncus hallii*, *Poa fendleriana*, *Trisetum spicatum*, *Erythronium parviflorum* and several species of *Carex*.

The invertebrate fauna of the herb-shrub layer is comparatively scanty and is composed mostly of small Diptera and leafhoppers. There are recorded in the writer's notes 7 species of Diptera, 5 of leafhoppers, 1 psyllid, and 1 aphid. There are also 3 species of parasitic Hymenoptera, and 2 species of ants.

Diptera are the most abundant invertebrates of the herb-shrub layer, and constitute about 41% of the population. Leafhoppers comprise 30% of the total, and several other forms make up the rest. The high percentage of Diptera corresponds with the condition in the northern coniferous forests.

#### c. THE TREE LAYER SOCIETY

The tree layer is composed of the two dominant plants, the Engelmann spruce and the alpine fir. The latter species has the lower branches resting on the ground and these, eventually becoming buried, take root and send up shoots so that the trees tend to stand in clumps or bushes. This situation does not prevail so much in the Lower Montane forests. The tree layer, therefore, comes all the way to the ground. The Engelmann spruce also adopts this habit of growth to a lesser degree.

In the tree layer there were identified about 10 species of Diptera, 5 of spiders, 1 of leafhoppers, 2 of psyllids, 1 of aphids, and about 9 of parasitic Hymenoptera.

In the tree layer, Diptera again plays an important part, forming about 69% of the average invertebrate population. Spiders and parasitic Hymenoptera each make up 13% while leafhoppers only form about 2%. The spiders are proportionately less abundant than they are in the Lower Montane. Invertebrates of the trees are eaten by kinglets and Audubon's warbler and also by the chipping sparrow. Hairy and alpine three-toed woodpeckers gain a large part of their food by prying off flakes of bark. Small spiders and the cocoons of certain Lepidoptera have been found under this bark.

Invertebrates are so few in all of the layers that the collection data indicate practically nothing regarding their seasonal abundance. Mosquitoes of the genus *Aedes* hatch out in the numerous lakes and ponds of the area in early June. Many of these make their way into the forests and are there taken on the herb-shrub and tree layers. These insects last until about the middle of July. This seasonal appearance

of large numbers of mosquitoes is another point of general resemblance between the Upper Montane and northern forests.

## 2. THE LODGEPOLE SUBCLIMAX

The Lodgepole subclimax of the Upper Montane is coextensive with that of the Lower Montane. It is the first conifer stage following burns (Clements, 1910) and is the first forest tree to invade meadows bordering lakes (Fig. 5, C). The aspen subclimax does not occur in the Upper Montane in the Uinta Mountains. On Mt. Timpanogos and most of the Wasatch Mountains the lodgepole pine is absent, but in the northern Wasatch it occupies the same position as it does in the Uintas.

No extensive investigation was made of the Lodgepole subclimax in this study, but from general observations it would appear that insofar as major and minor influents are concerned it is essentially like the adjoining climax. In some places especially in young stands the trees grow so close together that there is practically no undergrowth. This condition undoubtedly influences the animals of the lower socies, but the details of this have not as yet been worked out.

## 3. THE SPRUCE-FIR SUBCLIMAX

(*Picea engelmanni*-*Abies lasiocarpa* Associates)

The Spruce-Fir subclimax (Fig. 5) comprises practically the entire Upper Montane forest on Mt. Timpanogos. Such communities have been called "Physiographic Climaxes" by Tansley (1935, p. 292), but would undoubtedly fall under the term subclimax as applied by Weaver and Clements (1938, p. 81). Perhaps the term psysiographic subclimax might be appropriate here.

These Upper Montane subclimaxes occur over great areas in the Rocky Mountains and are extremely important features of the general bio-ecology of the areas in which they occur.

The factors that are responsible for this subclimax are combinations of physical forces common to steep and rugged terrane that is often found in the higher elevations of mountains. These physical forces may be summarized as follows:

1. *Instability of slopes due to steepness.* In many places the soil and loose rocks are continuously shifting due to the force of gravity, water, frost, and animals, so that it is difficult for even pioneer plants to gain a foothold and stabilize the community.

2. *Great areas of exposed rock surface.* Sheer cliffs often hun-

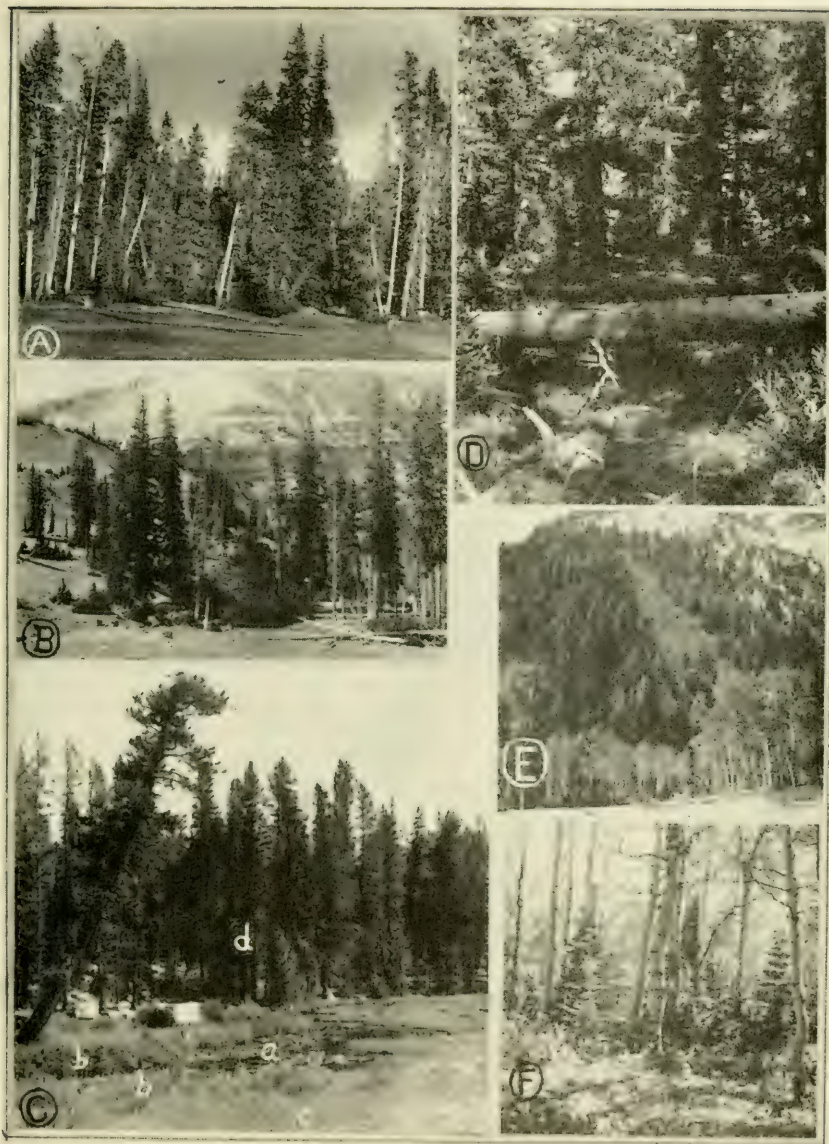


Fig. 5. A, Climax Upper Montane forest with subalpine meadow in foreground near Lost Lake, Uinta Mountains. B, Subclimax Upper Montane forest showing open growth, rim of Timpanogos Cirque. C, Succession stages in Upper Montane forest near Diamond Lake, Uinta Mountains: (a) water lilies in pond, (b) *Vaccinium* and willow bordering water, (c) sedges and grasses, (d) lodgepole pine subclimax. D, Floor of climax Upper Montane forest, Uinta Mountains. E, Lower Montane climax showing cottonwoods and aspens bordering the stream in foreground, Aspen Grove, Mt. Timpanogos. F, Aspen replacement by conifers (*Abies concolor*), near Aspen Grove, Mt. Timpanogos.



dreds of feet high are devoid of most vegetation except lichens and mosses in favorable places.

3. *Snowslides and landslides*, persistent over large areas, prevent the growth of forests by continually sweeping them off and allow only shrubbery or herbaceous vegetation to gain a permanent foothold. In winter on Mt. Timpanogos snowslides are almost continuous and devastating to tall vegetation.

4. *Length of time the snow is on the ground* is an important factor. On the high altitude Timpanogos cirques, prevailing winds from the west pile snow to a depth of many feet and in early summer these piles are effectively shaded by surrounding cliffs. As a result some patches of snow remain throughout the entire summer and a third to a half of the ground may be covered with snow until the middle of July (Fig. 12, A). The growing seasons, therefore, are very short (not more than two months) and the growth of trees is prevented even where altitude and soil conditions would normally permit the development of forests. As a result, in places that are free from snowslide action the growing season is so shortened due to persistence of snow that trees are able to grow only on exposed ridges where the snow cover leaves earliest in the summer.

5. *Fire* resulting either from human agencies or lightning is another factor that modifies these Upper Montane Forests. Judging from the vicious thunder storms that play around these high peaks in summer, trees standing on exposed ridges may be frequently struck and set afire. As a result, many trees, fire scarred and dead remain standing. Following such fires the Engelmann spruce seems to be slower to recover, but the alpine fir, being able to produce vegetatively, grows up to form dense and scrubby mats around the bases of dead or living trees that have escaped the fire.

Aside from the physical factors mentioned above, the generally well drained slopes and limestone substratum tend to make the soil less acid than in the Uinta Mountains, and as a result a number of the typically acid-loving plants such as *Vaccinium*, *Kalmia* and *Ledum* are absent.

The total effect of all of the above mentioned forces is to produce a vegetative aspect that is strikingly different from the extensive climax forests of the Uinta Mountains. The dominant trees, where they occur at all, are found as small open groves or as single individuals. The Engelmann spruce appears to cope best with these conditions and often grows to considerable size, but the alpine fir, except at lower elevations and in protected places, presents generally a krumholz as-



pect growing in stunted and densely matted clusters a few feet high.

Occupying steep slopes between the trees in many places is a luxuriant growth of shrubby and herbaceous vegetation in all stages of development through both hydroseres and xeroseres. The slopes are usually well watered at least during the early summer by the run off from melting snows and in winter they are completely covered by snow and swept with snowslides.

The net effect upon the animals of the community resulting from the conditions described above is at least twofold:

1. An increase of animal populations in all groups which is generally indicative of a subclimax or earlier seral stage.
2. Certain animals, typical of climax Upper Montane Forests are quite or nearly absent from the community. The red squirrel, for example, is rarely encountered in these communities; while such birds as the Rocky Mountain jay, Rocky Mountain pine grosbeak, Bent crossbill and alpine three-toed woodpecker have not been found.

On the other hand, the general climatic conditions, coupled with the presence of the dominant trees and the great majority of animal species shows the undoubted relationship of this community with the Upper Montane Forest in general, and in other portions of the Wasatch range, where conditions are more stabilized and less rugged, climax forests do develop. The study of the Spruce-Fir subclimax as it occurs on Mt. Timpanogos was carried out on the rim of Timpanogos cirque at an elevation of about 9,800 feet. This area was known as station 4. It represents actually the upper limit of the community which occurs here at a lower elevation due to the great accumulation of snow on the cirques as described above. It borders, therefore, the Alpine Meadow and has the appearance of an ecotone. The station, however, was representative of the subclimax forest and from the standpoint of animals possessed none of the characteristics of the Alpine Meadow.

#### a. GROUND LAYER SOCIES

The ground layer of the Upper Montane subclimax has much the same character as that of the climax. The soil forms little more than a veneer over the rocky substratum. There is a thin layer of conifer needles and in many places fallen logs are much in evidence. In pH reaction the soil is about neutral on Mt. Timpanogos. Growing over the surface are a number of mosses, particularly *Polytrichum*, and a few foliose lichens.

Invertebrate populations are extremely low as they are in the

Upper Montane climax of the Uintas. Two species of mollusks, 2 of centipedes, 5 of spiders, 4 of beetles, and 3 of ants have been identified. There were also some undetermined mites, and other small animals.

There was an average of only 16 animals per square meter in exposed places. Of these, 50% were beetle and Diptera larvae, 25% were mites, 12% ants, and 12% beetles. The beetles found in open places were mostly small Staphylinidae. The percentage of ants is somewhat higher here than in the climax Upper Montane, presumably because of a dryer condition due to more exposure to the sun.

Mollusks were more abundant under logs than in the climax Upper Montane. This seems to be correlated with less acidity in the soil and a greater supply of material for the construction of the shells. As has been previously explained, the rock substratum on Mt. Timpanogos is almost entirely limestone.

#### b. HERB LAYER SOCIES

This layer consists of a rather luxuriant growth of herbaceous plants. The most common species are *Lupinus alpestris*, *Clematis pseudoalpina*, *Mertensia leonardi*, *Aquilegia caerulea*, *Bistorta bistortoides*, *Leptotaenia multifida*, *Castilleja sulphurea*, *Pentstemon whippleanus*, *Cirsium lanceolatum*, *Trisetum spicatum*, *Festuca kingii*, *Bromus polyanthus*, and *Carex festivella*.

Large numbers of insects are found in the herb layer. There are at least 7 species of beetles, 8 species of Hemiptera, 10 of Diptera, 5 of leafhoppers, 4 of aphids, 2 of ants, and 11 of parasitic Hymenoptera that have been identified.

A small leafhopper, *Dikraneura carneola*, is exceptionally abundant and flies up in great swarms as one walks through the herbs. All species of leafhoppers together form 53% of the samples of invertebrate populations, aphids comprise 20%, and Hemiptera 10%. Hemiptera and Homoptera together form about 83% of the total population. Diptera make up only 7% of the total.

The total herb population in the Upper Montane subclimax was greater than that of corresponding layers in any other community studied (Fig. 10). It was about 8 times greater than that of the climax Upper Montane in the Uintas. Light is probably an important factor here in making possible a more luxuriant growth of herbs and favoring a higher population of invertebrates. This factor may also have an effect directly upon the organisms, but this would require experimental verification.

## c. SHRUB LAYER SOCIES

This layer appears as a definite undergrowth where trees are sufficiently abundant to be called a forest, and forms the most prominent part of the vegetation where trees are lacking and areas swept by snowslides. In the vicinity of station 4 of this study such shrubs as *Ribes cereum*, *Sambucus microbothrys*, *Potentilla glomerata*, *Dasiophora fruticosa* and *Salix sp.* are the most prominent.

Invertebrates found in this community include at least 6 species of beetles, 3 of Hemiptera, 6 of leafhoppers, 5 of Diptera, 2 of ants, and 9 of parasitic Hymenoptera.

Invertebrate populations on shrubs are only about a third as great as those found on the herbs according to the data thus far obtained. Leafhoppers are again the most prominent and form about 60% of the total population. Hemiptera make up 10%, ants 6%, Diptera 6%, beetles 4% and parasitic Hymenoptera 5%.

## d. TREE LAYER SOCIES

The scattered nature of the dominant trees in the subclimax has already been described.

Invertebrates that have been identified from the tree layer consist of 3 species of spiders, 6 of beetles, 12 of Diptera, 3 Hemiptera, 5 leafhoppers, 2 psyllids, and 9 Hymenoptera.

Leafhoppers make up 60% of the total population and Diptera are represented to the extent of 15%. Spiders comprise only 1% which is in sharp contrast with the 37% of the Lower Montane climax. This difference is evident in numbers as well as percentage. In the Lower Montane there was an average of 9 times more spiders than in the Upper Montane subclimax. The actual number of Diptera was the same in the Upper as in the Lower Montane but the percentage was much less in the former. In comparison with the climax Upper Montane of the Uintas the actual number of Diptera was somewhat higher, but the percentage was again much less in the subclimax. The total invertebrate population in the tree layer of the subclimax Upper Montane was about 6 times that of the climax (84 as compared to 15 per square meter).

Insofar as the seasonal data are significant, there appears to be a general increase in populations from June until September. The increase in leafhoppers which is rather uniformly seen in all of the layers shows the most regularity. This increase would seem to be associated with a corresponding maturing of the plants. Diptera show a great irregularity in numbers but on the whole tend to decrease

somewhat as the season advances. Large numbers of Hemiptera appeared on the herb layer in July, but disappeared again in August and September. These were mostly nymphs of the family Lygaeidae that could not be determined.

#### 4. INVERTEBRATE ANIMALS IN GENERAL

The invertebrates listed above in connection with the various communities represent in general the smaller species that are more or less confined to particular climax and subclimax communities. In addition there is a group of larger species that are usually not taken in quantitative samples. Many of these are confined to seral stages that are not included in this study, but others fly freely over or into the climax and subclimax stages or live in the wood of trees.

Butterflies and large Hymenoptera are the more conspicuous of these groups. A partial list of the butterflies is given in the appendix.

Another group of insects of wide distribution and often of great importance in coniferous forests are the bark beetles of the genus *Dendroctonus* (Scolytidae). These have been listed and discussed for the Utah area by Kartchner (1928). When these insects occur in epidemic form they may completely destroy considerable areas of forests and thus exert an important influence in the community. Such epidemics are now in progress on the north slopes of the Uinta Mountains especially where the Black Hills beetle (*Dendroctonus ponderosae*) is destroying a large area of these trees estimated at four to five thousand acres.

The effect of these beetles have not been noticeable in the stations included in this study.

There are also a large number of wood boring beetles of the families Buprestidae and Cerambycidae that attack either living trees or trees in various stages of decay. The buprestid, *Dicerca prolongata* attacks cottonwood and cherry and appears to be confined mainly to seral stages and the shrub layer of the Lower Montane. *Buprestis fasciata langi* and *B. maculativentris rusticorum* are known to mine dead and dying Douglas fir, white fir, alpine fir, and yellow pine in this area. These two species are distributed throughout the northern as well as the montane coniferous forests. *Chrysophana placida* lives in the cones and wood of live yellow pine, Douglas fir, white fir and alpine fir and appears to be confined mainly to the Montane Forests.

A number of cerambycid or long-horned wood boring beetles is also found in the localities of this study. *Monochamus scutellatus*, *M. oregonensis*, *Pachyta liturata*, *Neoclytus muricatulus*, and *Trago-*



*soma deψsarium* all attack the Douglas fir as well as other conifers. The last three species also occur in the transcontinental coniferous forests. The common round-headed apple tree borer, *Saperda candida*, lives in wild cherry in the mountains; *Saperda calacarata* occurs in aspens; *Anoplodera chrysocoma* attacks the alder; and *Prionus californicus* is found in living and dead roots of cottonwood and alder.

The wood boring Hymenoptera (Siricidae) are also generally distributed in the montane forests. *Urocerus californicus*, *U. flavicornis*, *Sirex juvencus* and *Xeris morrisoni* are known to inhabit most of the kinds of conifers in the area.

### C. INFLUENTS OF THE MONTANE FORESTS

#### 1. MAJOR PERMEANT INFLUENTS

The major permeant influents include the larger mammals and birds that occur throughout both the Upper and Lower Montane. In general they occur in all successional stages as well as the climax but they may be more abundant in some stages than in others.

The Rocky Mountain mule deer (*Odocoileus hemionus macrotus*) is perhaps the most important of the major influents. The habits of this animal have been described in considerable detail by Dixon (1934) and also by Rasmussen (1941). Their findings apply well to the local animals insofar as the writer has been able to observe them. The deer is found in all vegetational stages from the chaparral upward through the montane forests and into the Alpine Meadow. It occurs in the montane forest principally in summer and early autumn and moves into the chaparral in winter.

Due to the rather luxuriant growth of herbs and shrubs on Mt. Timpanogos, the coaction of the deer on the summer range is not so evident as it is in some other localities. It appears, from repeated observations on the feeding of this animal, that it grazes a great deal upon herbs during the summer months when these foods are available. It has been noted definitely to feed on false solomon seal (*Smilacina sessilifolia*) the lupine (*Lupinus alpestris*) the geranium (*Geranium richardsoni*), thimbleberry (*Rubus parvifloris*) and the aspen (*Populus tremuloides*). Browsing on the aspen has been frequently observed and could undoubtedly be a significant coaction where deer populations are high and other foods not available. Nearly all of the undergrowth in the montane forests seems to be utilized, unless it is the *Vaccinium* of the Uinta Mountains which does not seem to be palatable to these animals.

Coactions of deer on conifers has been a problem of unusual in-

terest. There is circumstantial evidence in the area that the deer feeds to some extent on the terminal leaders of both species of firs, causing them to spread out and retarding their upward growth. This coaction is especially noticeable where seedlings of these trees are coming up under aspen forests. It is likely that the snowshoe rabbit is responsible for a certain amount of this work but the writer has never succeeded in separating the two or has he ever seen either, animal in the act of eating these trees. Dixon (1934) regards *Abies concolor* as of major importance as a deer food and states that *Pseudotsuga mucronata* is also eaten. Rasmussen (1941) has shown the effect of the deer on the yellow pine on the Kaibab Plateau of Arizona. He points out in this connection that the damage is done mostly in early spring before more palatable food is available. The possibility that sheep, which are grazed in considerable numbers over much of the Wasatch Mountains, may be responsible for part of the damage to young conifers should not be overlooked. However, Young and others (1942) show that in northern Idaho, damage to conifers was slight even in heavily grazed areas, and in such areas was due mainly to trampling rather than foraging. If this statement of Dixon is true for this area, the deer is surely a great factor in retarding the replacement of aspen forest by conifers since this coaction is evident over large areas. In such places fully 75% of the trees are damaged.

Population estimates of deer at the stations studied has been particularly difficult due to the steepness of the hills and the density of the vegetation. The general observation gained from records of animals seen in the process of field work has indicated that they are fairly evenly distributed over the entire Montane Forest in early summer but that in August and September they tend to concentrate at higher altitudes.

On three successive trips to the American Fork cirque covering a distance of about 4 miles the following numbers were seen: August 9, 11; August 12, 12; August 15, 5.

This undoubtedly represents but a very small percentage of the animals actually present along the trail, for the way leads through brush of great density. The tracks and droppings of deer are everywhere abundant along trails or near watering places, but the effects of their feeding are often difficult to distinguish from those of the domestic sheep.

Deer appear to be more abundant at the present time on Mt. Timpanogos than they are in the Upper Montane of the Uintas. It seems likely that this may always have been the case since there is far more

of the palatable food at all elevations on Timpanogos. As has been previously stated the deer does not seem to browse extensively, if at all, on the species of *Vaccinium* which form a large part of the undergrowth in the higher portions of the Uintas. Dixon (1934) does not include this genus in a long list of plants eaten by the mule deer in California.

The American Wapiti ("elk") (*Cervus canadensis canadensis*) formerly occurred naturally on Mt. Timpanogos as is evidenced by remains of the animal found in caves. It is not known exactly when they disappeared from the area, but they have recently been restored as a small herd on the west side of the mountain. The history of the herd is given in a letter from the Utah State Fish and Game Department as follows:

"The Timpanogos elk herd had its origin in 1925 when one spike bull and eight cows were released. No hunting was permitted until 1932 when eight permits were issued for mature bulls and seven animals were killed. In 1933 six more bulls were killed; 1936 five bulls and 22 cows were trapped and transplanted in other areas. In 1937 eight bulls and eight cows were killed. The herd now (1939) numbers about 25 head."

There has been little opportunity to observe these animals, but they are so restricted in numbers and area that they are of little importance to the communities as a whole.

The Rocky Mountain Bighorn (*Ovis canadensis canadensis*) has been reported in the early literature for Mt. Timpanogos (Barnes, 1927, p. 175), and remains of this sheep have been found in American Fork Canyon caves. However, none of the animals occurs on the mountain at the present time.

The larger carnivores which may in the past have been considered as major influents have now largely disappeared from the area. Judging from the common occurrence of claw marks on the trunks of aspen trees the black bear (*Euarctos americanus* spp.) must formerly have been quite common on Mt. Timpanogos, and a few are to be found there to the present day. In about seven years of field work on the mountain the writer has seen only one, but there are reliable reports of several others. This information points to the existence of at least three of the animals on the mountain in 1937. One was also reported for the summer of 1941. Reliable reports indicate that there are still a few bear in the Uinta Mountains but no actual figures are available.

The Great Basin coyote (*Canis latrans lestes*) has been seen or heard at all stations on Mt. Timpanogos and at Lost Lake in the Uintas. It roams throughout all of the communities of the mountains both in summer and winter. Droppings and other signs are frequently encountered in the course of field work. It appears that in common with

	Conifer Climax	Aspen Subclimax
Mountain Shrew		
Black Bear		
Nevada Weasel		
Badger		
Coyote		
Uinta Bobcat		
Uinta Ground Squirrel		
Uinta Chipmunk		
Wasatch Least Chipmunk		
Red Squirrel		
Flying Squirrel		
Uinta Pocket Gopher		
White-footed Mouse		
Bushy-tailed Woodrat		
Red-backed Mouse		
Cantankerous Vole		
Utah Jumping Mouse		
Snowshoe Rabbit		
Mule Deer		

Fig. 6. Mammal distribution in conifer climax and aspen subclimax in Lower Montane forest.

its habits elsewhere the food of the coyote consists mainly of the small rodents common to the region. Carrion is also eaten where it is available.

The long-tailed red fox (*Vulpes macroura*) probably occurs in small numbers throughout the mountains, but the writer has no direct evidence of it in the areas studied.

Badgers (*Taxidea taxus taxus*) should probably be considered among the major influents of mountains since they are present at all elevations. Their food consists of Uinta ground squirrels and Uinta pocket gophers which they dig out of their burrows. On the basis of records that the writer has kept in covering large areas of Mt. Timpanogos there would appear to be about 3 of these animals per 10-acre area.



The mountain bobcat (*Lynx uinta*) is still to be found in small numbers according to reports. A sheepherder showed the writer two skulls and skins of bobcats taken in the Lower Montane, and there is evidence that they are present in the Upper Montane also. There is no direct evidence available as to their food habits in that area.

The Rocky Mountain marten (*Martes caurina origenes*) is probably of sufficient importance to be included with the major influents. This animal was formerly quite common in the Upper Montane Forests of the Uinta Mountains. It is arboreal to a considerable degree and seems to be confined mostly to the climax forests. The writer has no reliable information that it occurs in the Lower Montane Forests but it is likely that it does so. Trappers who are familiar with the habits of the animal have told the writer that they frequently burrow in the snow in winter and apparently travel long distances. It also appears that they fluctuate somewhat in numbers from year to year.

Habits of the marten in the Uinta Mountains have been studied by W. H. Marshall of the Fish and Wildlife Service, but the results of his findings are not as yet available. The stomach of an animal that the writer was able to examine contained the feathers of an unidentified bird.

Of the larger carnivores that formerly inhabited the area, the following are nearly or quite extirpated: Grizzly Bear (*Ursus horribilis bairdi*), wolf (*Canis lupus youngi*), cougar (*Felis oregonensis hipolestes*), and the wolverine (*Gulo luscus*). The cougar may still be present in very small numbers, and the wolverine has been reported north of Mt. Timpanogos in recent years. The others apparently have entirely disappeared.

Of the larger rodents of the Montane Forests, the yellow-haired porcupine (*Erethizon epixanthum epixanthum*) should be classed as a major influent. This animal is found mostly in climax and sub-climax forests, but it also wanders into shrubby seral stages and even onto the Alpine Meadow.

In the conifer forests the principal foods in winter are the white fir, alpine fir, lodgepole pine, and Engelmann spruce. The writer has seen no evidence of its feeding on the Douglas fir. Of the trees used as food the firs are preferred above all others but the lodgepole pine is also greatly favored. The Engelmann spruce is taken only rarely in this region. In addition, most of the larger shrubs common to the region are utilized. The writer has never found any sign of its feeding on the aspen.

In the extensive aspen forests of Mt. Timpanogos, the porcupine

plays an important role with the deer and snowshoe rabbit, in retarding the replacement of the aspen by white fir. In the vicinity of station 2 the writer has found that out of 41 seedling firs in a half acre plot, 32 (78%) were damaged to the extent that they would probably fail to reach maturity. This, however, would represent an extreme rather than an average condition. The feeding was all done in one year and probably by a single animal. In the Lower Montane Forest at Aspen Grove (station 1) fully half of the remaining white firs have been girdled near the top but not completely killed. It is rare to see a lone conifer tree in the aspen forest that has not been so attacked. In the climax forests young white firs are nearly always girdled near the ground and completely killed. It is, therefore, not inconceivable to the writer that in time this tree may be completely eliminated by the coaction of the porcupine.

On the basis of animals counted in the field it is estimated that there is about 1 animal per hectare in the Lower Montane climax and not more than half that many in the Upper Montane.

The golden-mantled marmot (*Marmota flaviventris nosophora*) is confined almost entirely to the early stages of the xeroseres and it is seldom found in the climax forests. Furthermore, its activities are limited to about five or six months of the year. It is doubtful as to whether or not it should be called a major influent since it probably effects the forests very little. It is most abundant in the Upper Montane and alpine regions especially on Mt. Timpanogos, but it extends into the Lower Montane and even downward into the valley grasslands to some extent.

The Rocky Mountain snowshoe rabbit (*Lepus bairdi bairdi*) is a common mammal throughout the montane forests. It reaches its greatest abundance in climax forests but is also present in many of the seral stages.

Baker and others (1921) have indicated that the rabbits do considerable damage to seedling conifers of all kinds by cutting off the shoots. According to these writers this damage is done in the winter when herbaceous vegetation is not available. As explained above there is evidence that the deer has this same coaction and it is difficult to tell which of the animals is responsible in any case. Seedlings four or five feet high are frequently attacked in this way, but it would be entirely possible for the rabbit to do this in winter when the snow is deep. In areas where the alpine fir is invading the aspen forests, the writer has noted that the tips are cut off from nearly a hundred per cent of the young trees. In spite of this coaction it appears that the

trees are eventually able to grow out of reach of the animals. The process seems to be one of retardation rather than complete arrestment of plant growth.

Relative numbers of rabbits have been arrived at principally by

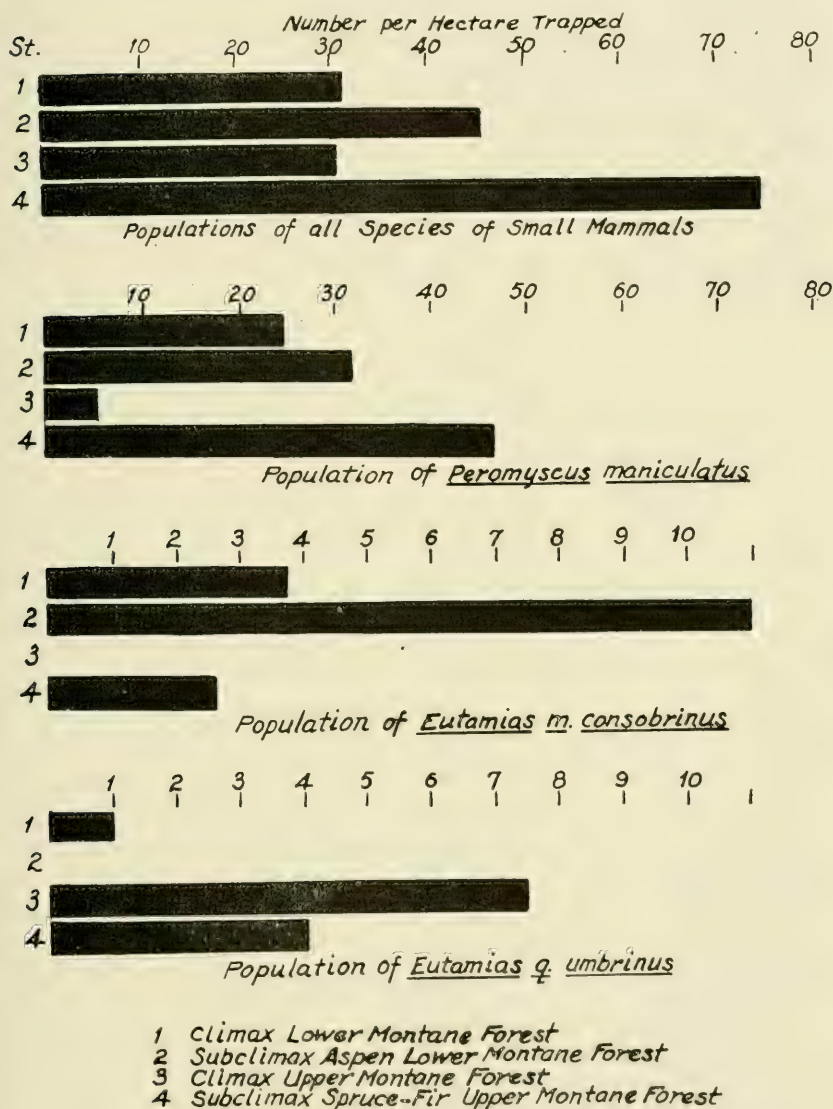


Fig. 7. Relative mammal populations as shown by plot trapping at stations in the coniferous forests.

scat counts. The animals are so secretive that they are seldom encountered in the woods even though they may be fairly numerous. Scat counts made at several of the stations show averages as follows:

	No. Per M <sup>2</sup>
Lower Montane Climax.....	10
Aspen Subclimax .....	2
Upper Montane Climax.....	16
Upper Montane Subclimax.....	16.2

This would indicate that the animals are about equally distributed where conifers occur with slightly greater populations at higher elevations. The counts in the aspen subclimax were made where there were a number of seedling conifers and the scats were usually found near there.

With one exception, the major influent birds found in the Montane Forests range also into the valley grasslands wherever there are suitable places for them to nest.

Perhaps the most abundant representative of this group is the Montana horned owl (*Bubo virginianus occidentalis*). This bird occurs in considerable numbers throughout all of the montane forest area. It begins nesting about the middle of March, and constructs its nests either in trees or on cliffs. The abandoned nest of some hawk is generally utilized, and nesting pairs will use the same site for many years.

Examination of horned owl pellets indicates that their food consists of most of the common rodents of the region including *Citellus*, *Microtus*, snowshoe rabbit, *Peromyscus*, and *Neotoma*. Hunting is usually confined to late evening and early morning just before dark and at dawn. However, the birds occasionally forage by day. At Lost Lake, while the writer was observing a pair of half grown young at 3 P. M. on June 18, 1940, the parent came in carrying a full grown pocket gopher. This not only proves the daytime activity of the owl but shows that the gopher was out of the burrow in the daytime. The weather record indicates that the day was cloudy.

The golden eagle (*Aquila chrysaetos canadensis*) is found in small numbers on Mt. Timpanogos and one has been seen in the vicinity of station 3 in the Uintas. The nests seem to be located so that each pair of birds has a feeding radius of at least three to five miles. Nesting sites are usually on high cliffs but are occasionally built in large trees. Remains about the nests indicate that the marmot and snowshoe rabbit form a large share of the food, as well as rabbits from the valleys. A dusky grouse was found in one of the nests.



Another predator found throughout both the Upper and Lower Montane is the Western red-tailed hawk (*Buteo borealis calurus*). This species also nests on cliffs and large trees. The food consists mostly of small rodents. A stomach of one taken at Lost Lake (station 3) was filled with mammal hair presumably of *Microtus* and *Thomomys* and contained the claws of *Thomomys*.

The only one of the larger predatory birds that appears to be purely montane in distribution is the Eastern goshawk (*Astur atricapillus*). This species usually chooses dense woods for nesting sites, and builds the nests either in aspens or conifers. The food of this hawk is mainly rodents but it often takes grouse and other large birds. A nest was under observation in the Lower Montane climax at Aspen Grove for two years. It was noted many times that the activity of these noisy birds in this forest seemed to bother most of the small birds very little. The adults were often seen returning to the nests with squirrels apparently obtained well outside the forest. Red squirrels always show considerable concern when the hawks are about and possibly are used for food. However, the writer has no positive evidence of this.

The osprey (*Pandion haliaetus carolinensis*) often occurs in Montane Forests. None has been seen on Mt. Timpanogos, but near Lost Lake in the Uinta Mountains one had its nest in the top of a large Engelmann Spruce for a number of years. The birds were frequently seen catching fish from the mountain lakes in the vicinity.

## 2. MINOR INFLUENTS

Minor influents include the smaller mammals, the great majority of the birds, and the reptiles and amphibians.

About two species of smaller carnivores may be included in this group. These are the Nevada weasel (*Mustela frenata nevadensis*) and the Great Basin striped skunk (*Mephitis occidentalis major*). The former occurs in scattered numbers throughout the Montane Forest and appears in all the vegetational stages. Frequently the weasel is encountered during the daytime but it is mostly nocturnal. It feeds upon most of the small rodents especially the nocturnal mice and will also attack ground-nesting birds. Evidence of the destruction of several juncos, apparently by this animal, have come to the attention of the writer.

The striped skunk appears to be quite rare in the area studied, but the writer has found some evidence of them in all stations. Characteristic odors of the animals are noted occasionally about Aspen Grove (station 1) and a skull of one was picked up in the Upper Montane

on Timpanogos cirque. Skunks are generally known to be omnivorous feeders, but no specific data are available for this area.

The Uinta ground squirrel (*Citellus armatus*) is the most conspicuous of the minor influents on Mt. Timpanogos in summer. It ranges from the chaparral ecotone into the montane forest and extends upward to the alpine meadows. In the Upper Montane of the Uintas it is far less common, but is nevertheless present in open spaces and at the forest edge.

Figure 8 shows graphically the relative activities of this animal on Mt. Timpanogos at two elevations during the summer of 1940. These curves would vary somewhat from year to year depending upon the amount of snow, which governs to some extent the time that the animals appear in the spring. It will be noted from the figure that the animals come out of hibernation in April at lower elevations and in June at higher levels. At the lower stations hibernation does not begin until the early part of July but it is completed by the middle of August. At higher stations hibernation begins somewhat later and is not completed until about the first of September. Activity is in general correlated with the period of most succulent vegetation upon which the animals chiefly feed. Hibernation occurs in underground burrows to a depth of one to two feet. A nest composed mostly of dry grasses is placed in a slight enlargement near the end of the burrow. When the animal emerges in the spring it apparently burrows nearly straight up from the nest often through several feet of snow. The young are born underground and appear above the surface when about one third grown. June 3, 1941 is the earliest record that the writer has of the appearance of young of the year at the Lower Montane level. It apparently takes two years for the animals to reach full size.

Where ground squirrels are abundant they form well beaten paths through the vegetation. These paths lead over whatever obstacle may be in the way including shrubs 18 inches in height. The animals have not been noted to climb trees but are often seen sitting in shrubs several feet from the ground. They often eat the tender twigs and berries of these shrubs.

Succulent herbs appear to constitute the chief food of the ground squirrel. The more tender portions of the plants are most sought after. When the animals emerge in the spring they feed principally on the tender tips of the plants as they appear above the ground, or where the plants are not yet up they will dig for them. Shallow holes an inch or so in depth are commonly seen in early spring. Later in the season when the herbs become taller the squirrels bend them down in

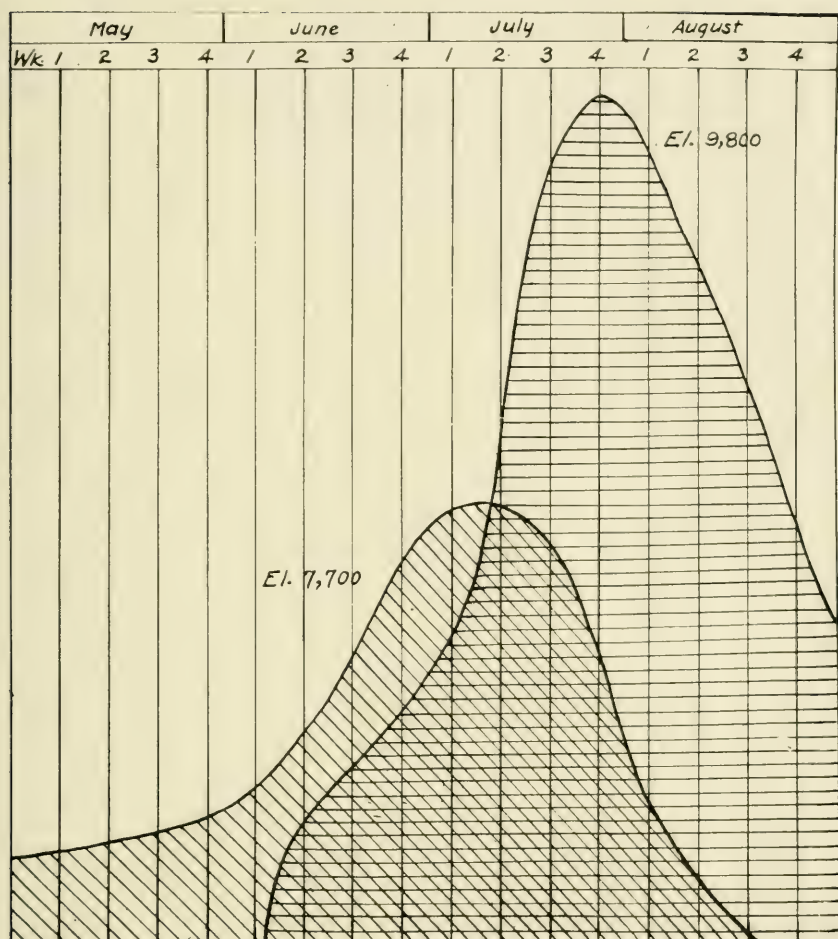


Fig. 8. Graph of seasonal activities of *Citellus armatus* at two elevations on Mt. Timpanogos.

order to get at the terminal portions. These animals are by no means strictly herbivorous but readily eat flesh when it is available. Smaller mammals caught in traps are frequently eaten by them and the writer has often seen them eating their own kind.

The Uinta ground squirrel reaches its greatest populations in early seral stages, but they are also very common in the aspen subclimax. They enter the Lower Montane climax to some extent but seldom penetrate in the Upper Montane climax. In the Uintas they are un-

common at high elevations even in seral stages but a few occur in open areas and along roadways.

Populations were arrived at by counting burrows and by keeping records of small traps sprung by them in small plots. Data compiled from these counts show relative populations as follows:

	No. Burrows Per Hectare	Percentage of Small Traps Sprung
Lower Montane climax	24	9.0
Aspen subclimax	34	17.0
Upper Montane climax	3	0.5
Upper Montane subclimax	30	19.0

These data coincide with the general observations that the animals are most abundant in the subclimax stages and much less common in the climaxes. The above data on number of traps sprung offers an interesting method of obtaining information on relative as well as seasonal populations. Undoubtedly a small portion of this trap springing is due to other species of mammals, but records of trapping when the squirrels were in hibernation indicate that this amounts to less than one per cent.

Two species of red squirrels are found in the area under discussion. *Tamiasciurus fremonti fremonti* is found in the Uinta Mountains; while *Tamiasciurus hudsonicus ventorum* occurs in the Timpanogos region. The two species occur together in the western Uintas. Both appear to have essentially the same habits. Certain minor differences, probably associated with local conditions will be pointed out in the course of the discussion.

The red squirrel is distributed throughout both Upper and Lower Montane climax forests, but it rarely occurs in the scattered subclimax condition found in the Upper Montane of Mt. Timpanogos. This squirrel seldom enters deciduous woods in this region unless there is a considerable mixture of conifers. Patches of alpine fir an acre in area in the midst of aspen forests generally contain red squirrels, but they are rarely found in smaller groves.

These squirrels are more or less active the year around. Young are born in June at which time the females are secretive and seldom appear in the open. Of ten specimens taken in the Lower Montane in June only one was a female. This individual had eight active nipples. A female taken in the Upper Montane June 19 contained six embryos measuring 17 mm. Young squirrels do not appear until late summer when they are nearly full grown.



Nests are constructed either in hollow trees or on the branches outside. The Fremont squirrel of the Uintas apparently uses hollow trees entirely, for the writer has never come across an outside nest. Outside nests of *ventorum* are common in the Lower Montane of Mt. Timpanogos. These nests are usually placed from 10 to 25 feet from the ground in the Douglas fir. They are generally a foot or more in diameter with an outer shell composed mostly of long shreads of bark from the ninebark, and an inner lining of fine plant fibers. Apparently these outside nests are used mostly as sleeping quarters, since many of them have been opened during the breeding season without finding any young.

The principal food coactions are centered around the conifers. In the Lower Montane the Douglas fir appears to be used exclusively. There is no evidence of the use of the white fir seed for food in that area. In the Upper Montane all of the conifer species are used but the Engelmann spruce is preferred. Storage of cones for winter use begins about the middle of July and coincides in general with the appearance of the young squirrels of the year as well as the maturity of the cones. Cones are usually cut early in the mornings and then stored away gradually during the day. As many as a half a bushel of cones may be cut from a single tree in a morning. Storage takes place either in hollow trees or in large midden piles at the base of the trees. In the latter case they are packed close together in burrows in piles of cone fragments.

During this time a great many seeds of fresh cones are eaten and little piles of cone fragments may be seen most anywhere on limbs or logs that appear to be favored spots for feeding. Elsewhere (1940) the writer has published an account of these feeding habits and shown that large numbers of cones are used in this manner.

Besides conifer seeds, red squirrels frequently store mushrooms and feed on berries. Hatt (1929) states that in winter they eat the terminal buds of the conifers.

The effect of the red squirrel in the recovery of forests following burns has been discussed by Hofmann (1920). It is known that cones stored by the squirrel may be viable for a long time and reforest an area if the burns are not too deep. It would appear from the great feeding activities of the squirrels, particularly in autumn, that nearly all of the produce of the trees would be utilized at that time or during the winter. It was noted, however, in the Lower Montane of Timpanogos, that during the favorable summer of 1941, literally thousands of seedlings of Douglas fir were coming up on the forest floor, indi-

cating that the coactions of the squirrels were not sufficient to prevent the renewal of the forests provided other conditions were favorable.

Two incidents of mass migrations of red squirrels from mountains to valleys have been observed by the writer in the Bear Lake Valley region of the northern Wasatch. The first took place about 1916 or 1917 when large numbers of squirrels appeared in the deciduous trees about the towns and villages, and remained throughout one winter and summer. Another similar movement occurred in 1942. The 1942 activity was coincidental with a very dry summer in the mountains, but no study was made to determine whether or not this was the responsible factor.

Populations of red squirrels at the various stations have been difficult to estimate. It has been done mainly by watching for and listening for individuals in a known area at times of greatest activity. On the basis of such observations the writer has estimated 25 per hectare for the Lower Montane climax and 15 per hectare for the Upper Montane. There were no squirrels seen or heard at station four in the Upper Montane subclimax.

The Utah flying squirrel (*Glaucomys sabrinus lucifugus*) is found throughout the Montane Forest. It is apparently confined mostly to conifers but the writer has one record of its presence in a mixture of aspens and maple. These squirrels live mostly in hollow trees but are also supposed to construct outside nests somewhat after the fashion of the red squirrel. No such nests have been positively identified in this study.

Flying squirrels appear to be almost strictly nocturnal, but little is known regarding their food habits in this area.

Their numbers are difficult to estimate. Covering a two hectare area in Lower Montane climax on several consecutive nights with a Coleman lantern revealed one animal on each occasion seen in about the same place. In a similar area in the Upper Montane climax of the Uintas two animals were seen.

The pocket gopher (*Thomomys talpoides*) is found throughout the Montane Forests at all elevations. The reactions of this animal in the soil have been already referred to. They are active throughout the entire year burrowing underground in the summer and under the snow in winter.

They remain underground most of the time in summer, feeding upon the roots of many of the herbaceous plants. However, they frequently come out of their burrows and fill their cheek pouches with surface vegetation. Wherever there is a surface opening to the bur-

row there may be a circle of vegetation cut within a few inches of the hole. On certain occasions they seem to move away considerable distances from their burrows, since they have been caught in mouse traps 15 to 20 meters from the nearest mound.

When underground, the pocket gopher is quite safe from most enemies except the badger which can easily dig them out. When they leave their burrow or even expose a part of their body they are preyed upon by most of the predatory birds. Their remains are found with unexpected frequency in owl pellets, hawk stomachs and around nests. This must indicate that they leave their burrows more often than is usually supposed. Their poor eyesight must materially reduce their chances for escape.

Numbers of gophers have been estimated by counting fresh summer mounds over known areas. In early morning, mounds that have been raised during the night are still wet and it is an easy matter to determine whether or not the animal is active. Mounds usually run along in an irregular chain for several meters. Trapping experience indicates that one gopher is responsible for a series of mounds.

Populations ascertained in this way indicate that gophers are largely confined to mid-seral stages and the subclimax and are not so common in the climax forests. However, the nature of the soil for burrowing and the herbaceous growth appear to be more important determining factors than the nature of the climax. Favorite habitats are grassy meadows where the soil is not too dry. Loose soil, even though it may be quite rocky, is frequently used provided it is not too dry. Of the Montane Forest communities the highest populations were found in the aspen forests with an average of 17 per hectare and a maximum of 40. The Lower Montane climax had an average of 12 per hectare which is thought to be high since the counts were made in a fairly level place where there was a good growth of herbs. On steep hills where there is little herbaceous vegetation none occur. Only rarely were gopher diggings found in the climax of the Upper Montane although the animals were common in the earlier seral stages.

Another animal characteristic of the Montane Forests is the bushy-tailed woodrat (*Neotoma cinerea acraia*). These animals are most abundant in early seral stages and are principally found in crevices of cliffs or small caves. Under natural conditions they probably do not enter the climax forests to any extent, but where old buildings are available they will take up their abode in such places. They were seldom encountered in this study and very little is known of their habits or populations.

A number of species of smaller mammals of chipmunk size and smaller inhabit the entire Montane Forest and were found at all of the stations. They are as follows:

- Uinta Chipmunk (*Eutamias quadrivittatus umbrinus*)
- Wasatch Chipmunk (*Eutamias minimus consobrinus*)
- White-footed Mouse (*Peromyscus maniculatus ssp.*)
- Gale Red-backed Mouse (*Clethrionomys gapperi galci*)
- Cantankerous Meadow Mouse (*Microtus mordax mordax*)
- Mountain Shrew (*Sorex vagrans monticola*)
- Utah Jumping Mouse (*Zapus princeps utahensis*)

Of the two chipmunks, the Uinta seems to prefer the dense woods while the Wasatch is more abundant in brushy stages or open aspen woods. This, however, is not invariably the case. The Wasatch chipmunk (Fig. 7) comprises about 12% of the small mammal population in the Lower Montane climax, 23% in the aspen forest and about 3% in the Upper Montane subclimax. It was absent from the Upper Montane climax. In the latter case it is known to inhabit forest edges but does not penetrate far into the dense woods. The Uinta chipmunk was not taken in samples from the Lower Montane climax but it is known to occur there in small numbers. It was not collected in the aspen forests and the writer has never seen it there. This species comprises about 5% of the total small mammal population in the subclimax Upper Montane and 23% in the climax Upper Montane of the Uintas.

The principal food of both chipmunks appears to be seeds and fruits of which they eat a great variety. In high altitudes they are frequently seen eating the fruits of *Vaccinium* and the red gooseberry. The Uinta chipmunk often climbs trees and has been seen coming down an Engelmann spruce bearing a fully grown cone. Rather than cutting and dropping the cones after the manner of the red squirrel they carry them down in the mouth.

Seeds are frequently carried in the inside cheek pouches and are stored usually in underground dens. Chipmunks are more or less active during the winter but tend to stay in during severe weather.

*Peromyscus* (Fig. 7) is the most common small mammal found in the areas studied. In the Lower Montane climax it made up 80% of the total small mammal populations, in the aspen forest 66%, and in the Upper Montane subclimax 60%. In the climax Upper Montane of the Uintas, however, its numbers dropped considerably, forming only about 50% of the population. A fact of great interest here is that the lowest population is attained in the upper Montane Associa-



tion of the Uintas and the highest in the subclimax condition of the Upper Montane on Mt. Timpanogos.

TABLE 11

Population of species of small mammals per hectare trapped.

Numbers represent average summer (June to September) population for part of 1939, all of 1940, and part of 1941. Percentages are approximate and are in terms of total small mammal populations in each community.

	Lower Montane Climax		Aspen Subclimax		Upper Montane Climax		Upper Montane Subclimax	
	No.	%	No.	%	No.	%	No.	%
<i>Peromyscus maniculatus</i>	25.0	80	31.2	66.0	4.0	15.1	46.0	60.1
<i>Clethrionomys g. galei</i>	2.2	8	2.5	5.5	7.5	23.3	1.2	1.6
<i>Microtus m. mordax</i>	*	..	1.2	2.5	4.0	15.1	18.7	25.1
<i>Microtus m. nanus</i>	..	..	..	..	3.7	11.5	..	..
<i>Microtus r. macropus</i>	..	..	..	..	1.2	3.5	..	..
<i>Zapus p. utahensis</i>	..	..	1.2	2.5	..	..	1.2	1.6
<i>Eutamias m. consobrinus</i>	3.7	12	11.2	23.5	..	..	2.5	3.4
<i>Eutamias q. umbrinus</i>	*	..	..	..	7.5	23.3	3.7	4.9
<i>Sorex v. monticola</i>	*	..	..	..	2.5	7.7	1.2	1.6
Totals	30.9	..	47.3	..	30.4	..	74.5	..

\*Known to occur rarely but not taken in quantitative samples.

Examination of the collection data shows that the high populations in the latter case are attained during late summer and fall, at which time the numbers increase from 50% to 75% over early spring and summer. In the climax the populations remain about the same throughout the seasons.

The writer suspects that this late summer increase in the case of Timpanogos is due in part to influx from lower elevations. Due to the great steepness of Timpanogos as compared to the Uintas this would not involve nearly such a great travel distance. There has been no way to prove, however, the validity of this theory.

Peromyscus are essentially animals of the ground layer, although they are known to climb trees occasionally. All published records that the writer has seen indicate that they are strictly nocturnal, and this is almost invariably true. However, one was seen to leave its hiding place and wander away several meters on a bright warm day at 1 P. M. Others were seen to come out just after sunset when it was still light enough to see easily and wander about in search of food.

These mice appear to live mostly in the abandoned burrows of other animals. Their burrows and runways are not evident in these forests as they are in eastern deciduous forests. In looking over an area one wonders where so many mice are able to find hiding places. Apparently they do not use logs to any extent, for the writer has turned over many of these without finding a single nest or seeing a mouse.

Peromyscus is active and apparently breeds throughout the entire year with the peak of reproduction during the summer. The writer's own breeding records are all of summer and are as follows:

	No. of Embryos
April 7, 1939.....	4
May 1, 1937.....	5
June 23, 1937.....	4
June 30, 1937.....	5
August 1, 1940.....	5
August 1, 1940.....	7
Av. ....	<hr/> 5

Peromyscus apparently feeds upon most types of available organic matter but shows a preference for seeds. In the aspen forests the favored food is the seeds of the niggerhead (*Rudbeckia occidentalis*).

The Gale red-backed mouse was found at all stations in the Montane Forest. They were found in greatest relative numbers in the climax forests, forming 8% of the total small mammal population in the Lower Montane and 23% in the Upper Montane climax. Their

actual numbers in the aspen forests were the same as the Lower Montane conifers but their per cent of the total small mammal populations was less (Table II). These mice appear to show considerable fluctuations in numbers from year to year, and undoubtedly follow cyclic population trends common to many rodents. During the summer of 1930 it was noted that redbacks seemed to be unusually abundant. No quantitative trapping was done, but the animals were frequently encountered in the woods in daytime, and their runways were common about the stumps of trees. During the summer of 1934, no red-backs were collected on Mt. Timpanogos during the two weeks of trapping. In the early summer of 1937, from a total of about 1500 traps set in favorable places only three specimens or .02% were obtained. In 1939, Mr. James Bec, trapping on Mt. Timpanogos, took 24 specimens or .6% from 4000 traps. My own collecting during that same season showed a similar increase in abundance. In 1940 the collecting records show about the same relative numbers (.02%) as 1937, indicating a decline from the population peak. General observations over this 10-year period bear out the indications of the quantitative records.

The cantankerous meadow mouse is confined principally to early hydrosere stages in the vicinity of springs, bogs or streams. However, they do often appear in considerable numbers in subclimax and even climax stages. In the Upper Montane subclimax of Mt. Timpanogos they were found to the extent of about 19 animals per hectare trapped (Table II). This amounted to about 25% of the total mammal population. In the climax Upper Montane of the Uintas an average of 4 were taken per hectare trapped, but this was 15% of the total population. In the aspen subclimax there was only about one per hectare trapped, which amounted to only 2.5% of the population. No *Microtus* were taken in the sample plots in the Lower Montane climax, although the species has been caught there in qualitative collecting.

These microtines are extremely characteristic of mountain communities in general and have a very wide distribution. A favorite place for their nests is underground in the midst of a clump of willows or birch. These nests are composed of dry grass. Runways lead out from them in all directions. In winter the nests are often built under the snow in grassy situations and are generally abandoned when they become exposed.

Microtines are active by day as well as night and are an important source of food for most of the predaceous birds and mammals. The mountain shrew has been seen by the writer carrying young *Microtus* out of their runways.

The Utah jumping mouse appears to be nearly confined to the Lower Montane Forest. Svihla (1932) reports that in her study of the eastern Uintas, she found them confined to lower elevations, and the writer has not found them in the Upper Montane climax. However, they do occur in small numbers, in the Upper Montane subclimax on Mt. Timpanogos and also in the northern Wasatch. They are most abundant in the vicinity of water, but occur to the extent of 2.5% of the small mammal population in aspen forests.

Jumping mice have not been taken in sample plots in the climax Lower Montane, but they have been rarely collected there in qualitative trapping.

These mice are frequently active by day and it is not unusual to start them from the grass in the daytime. Unlike other mice of the area they hibernate in winter. In preparation for this they become exceptionally fat during the late summer. Hibernation seems to occur about the first of September.

One mouse, *Phenacomys intermedius*, appears, on the basis of present evidence, to be confined to the Upper Montane, but the animal is so rare that it is unsafe to postulate this too strongly. This animal was found in the Upper Montane subclimax of Mt. Timpanogos but was not taken in the climax forests of the Uintas. However, Hall (1931) reports that it was taken in the Uintas under essentially subclimax conditions.

The mountain shrew occurs in small numbers throughout the Montane Forest. It is most abundant near streams but ranges also into the climax forests. In the Upper Montane climax it made up nearly 8% of the total of small mammals and in the Upper Montane subclimax formed about 1.6% of the populations. This shrew was not taken in quantitative samples in the Lower Montane climax, but it has been trapped there in qualitative work.

At least two bats (*Myotis volans interior* and *Nycteris cinerea*) are found in scattered numbers throughout the montane forests.

Average small mammal populations are shown in figure 7. They are greatest in subclimaxes and least in climaxes. It will be noted that Lower and Upper Montane climaxes seem to have almost identical small mammal populations (about 30 animals per hectare trapped).

It will be noted from figure 6, that the great majority of the small mammals occur freely in both the climax (conifer) and subclimax (aspen) of the Lower Montane. The red squirrel seems to be strictly confined to conifers while other species are more or less restricted to one or the other of the communities.



A tabulation of the minor influent birds according to their known breeding distribution in the two Montane Associations is given below:

Species found in both Upper and Lower Montane:

- Turkey Vulture (also in valleys)
- Sharp-shinned Hawk (also in valleys)
- Cooper's Hawk (also in valleys)
- Prairie Falcon (also in valleys)
- Dusky Grouse
- Spotted Sandpiper (also in valleys)
- Red-shafted Flicker (also in valleys)
- Natalie's Sapsucker
- Rocky Mountain Hairy Woodpecker
- Northern Cliff Swallow (also in valleys)
- Utah Jay
- Clark's Nutcracker
- Mountain Chickadee
- Rocky Mountain Nuthatch
- Rocky Mountain Creeper
- Dipper
- Western Robin (also in valleys)
- Audubon's Hermit Thrush
- Townsend's Solitaire
- Western Golden-crowned Kinglet
- Eastern Ruby-crowned Kinglet
- Cassin's Purple Finch
- Northern Pine Siskin (also in valleys)
- Bent's Crossbill (not known to breed in Wasatch)
- Gray-headed Junco
- Pacific Nighthawk (also in valleys)
- White-throated Swift (also in valleys)
- Broad-tailed Hummingbird (also in valleys)
- Western Flycatcher
- Common Rock Wren (also in valley)
- Mountain Bluebird (also in valley)
- Rocky Mountain Audubon Warbler
- Western Chipping Sparrow (also in valley)
- Lincoln's Sparrow
- Slate-colored Fox Sparrow (also in valley)

Extending from the valleys up into the Lower Montane:

- Western Mourning Dove
- Batchelder's Woodpecker
- Western Wood Pewee
- Long-tailed Chickadee
- Western House Wren
- Western Warbling Vireo
- Rocky Mountain Black-headed Grosbeak
- Lazuli Bunting

Apparently confined to the Lower Montane:

Red-naped Sapsucker  
Hammond's Flycatcher  
Violet-green Swallow  
Tree Swallow  
Purple Martin  
Red-breasted Nuthatch  
Western Tanager  
Gray Ruffed Grouse

Apparently confined to the Upper Montane:

Alpine Three-toed Woodpecker  
Olive-sided Flycatcher  
Rocky Mountain Jay  
Rocky Mountain Pine Grosbeak

Birds whose distribution is uncertain:

Flammulated Screech Owl  
Rocky Mountain Pygmy Owl  
Lewis' Woodpecker  
Olive-backed Thrush  
Orange-crowned Warbler  
Calaveras Warbler  
Western Evening Grosbeak

It has been the writer's experience that "confined" lists tend to break down with continued field work, so that the above lists may require modification as time goes on.

The above lists of species may be tabulated as follows:

	No.	Per cent of Breeding Species
Found in both of the Montane associations and the valley.....	35	60.3
Throughout Montane but not in valley	19	32.7
In Lower Montane and valley only....	8	13.8
In Lower Montane only.....	8	13.8
In Upper Montane only.....	4	8.6
Distribution uncertain .....	7	

Minor influent birds of the montane forests show a wide variety of relationships with the communities (coaction) and the habitat (reaction). They may be divided into groups according to these interrelationships. In general it may be said that birds do not confine themselves to single vegetational layers but some portions of their life habits are connected with all or a number of the societies.

The dusky grouse and ruffed grouse are perhaps the most nearly confined to the ground layer of any of the birds. Their nesting and

inating occur on the ground and, in the case of the ruffed grouse at least, fallen logs are generally used for drumming. Much of the food of these birds is also gained by scratching in the ground after the fashion of all gallinaceous birds. Trees and shrubs are used, however, as places of refuge and the birds also often roost in such places. Fruit bearing shrubs such as service berry, blueberry, gooseberry, Oregon grape and chokecherry constitute a large part of the food in late summer and the buds of willow, alder, and most other shrubs are used extensively in winter. Buds of nearly all herbs are also used for food.

The ruffed grouse is essentially a forest edge bird, being confined mostly to aspen parklands of the Lower Montane. Bent (1932, p. 171) quotes M. P. Skinner as saying that these birds inhabit the coniferous forests in the Yellowstone Park and this has been noted by the writer also in the Lower Montane of the Uintas. The dusky grouse is also frequently found in climax forests but it inhabits seral stages more often. Nesting of both species normally occurs in May.

Four other birds of the Montane Forests are primarily ground dwellers. These are the gray-headed junco, Lincoln's sparrow, slate-colored fox sparrow and white-crowned sparrow. All of these species nest upon the ground primarily, although the white-crown and fox sparrows may nest in shrubs or bushes a few inches from the ground. Food of these birds is gained mostly from the ground in the form of seeds and invertebrates. The fox sparrow and Lincoln's sparrow will frequently scratch for food. Lincoln's sparrow has been seen eating aphids from willows.

Lincoln's sparrow and the fox sparrow are confined to willow thickets along streams or shrubbery growths in snowslide areas. They have not been seen to enter the climax forests. The junco and white-crowned sparrow are most often seen at the forest edge, but not infrequently they enter the climax forests and breed there. All of these species are summer residents only in the montane forests.

Another group of birds utilizes tree or shrub layers as nesting sites but feeds primarily on the ground. These are principally members of the thrush family including the western robin, Audubon's hermit thrush, Townsend's solitaire, olive-backed thrush and mountain bluebird. All of these feed mostly on animal matter taken from the ground layer during the early part of the summer. They turn to berries of most every kind in late summer, and the robin and solitaire in particular depend upon these all winter.

Audubon's hermit thrush and olive-backed thrush leave the area entirely in the autumn but robins, solitaires and to some extent blue-

birds merely shift to lower elevations, often in the chaparral, where food is available at all times.

The western mourning dove is primarily a bird of the valley grasslands and deserts, but the writer has found it breeding in aspen forests on Mt. Timpanogos and in Lower Montane conifers in the Uintas. The nests are built either in trees or on the ground, but the birds feed almost entirely on the ground.

Sharp-shinned and Cooper's hawks and the pygmy and flammulated screech owls also nest in trees and feed primarily from the ground layer. The two species of hawks, however, take a good portion of their food from trees in the form of small birds. They nearly always light in trees to eat their prey.

The two hawks mentioned above as well as the robin, and Audubon's hermit thrush are found breeding in all seral stages including the climax where there are shrubs or trees. The mountain bluebird lives mostly in aspens, at lower elevations, where it builds its nests in holes. In the Upper Montane it utilizes old woodpecker holes in dead conifers as nesting sites. The flammulated screech owl has been found so far only in aspens where it also nests in holes, while the Rocky Mountain pygmy owl seems to occur only in conifers. Townsend's solitaire nests on rock ledges or in brushy seral stages, and the olive-backed thrush seems to be confined to willow thickets along streams or near springs.

Another group of birds builds its nests in the trees and gains the major part of its food from the tree, shrub, and herb matrices, but it also feeds to a lesser extent upon the ground. This group includes the Rocky Mountain black-headed grosbeak, western house wren, red-shafted flicker, Cassin's purple finch, northern pine siskin, red cross-bill, Rocky Mountain jay, Rocky Mountain pine grosbeak, western chipping sparrow, and Clark's nutcracker.

The red-shafted flicker in addition to taking food from the tree matrix frequently feeds on the ground especially on ants. It generally nests in holes in trees but occasionally utilizes holes in earth banks. This bird frequently perches on trees or on the ground for long periods in contrast to most woodpeckers that cling almost exclusively to the trunks or branches. The black-headed grosbeak seems to be confined almost entirely to brushy areas or aspen forests. It is rarely seen in conifer forests and then perhaps only as a transient. Its food consists mainly of buds and berries. Berries of the red elderberry are eaten extensively by this species in autumn.

Conifer seeds form a large part of the food of the pine siskin espe-



cially in autumn and winter, but it also eats much plant and animal matter from other layers. It feeds extensively on the seeds of the niggerhead (*Rudbeckia*), gathering these both from the plants and from the ground.

Clark's nutcracker and the Rocky Mountain jay are confined to the Upper Montane during the summer and to a large degree in winter. Nesting of the nutcracker occurs in early spring (March and April) and may take place in either Upper or Lower Montane Forests. Bee and Hutchings (1942) recently reported the bird breeding in the Wasatch in Lower Montane. These birds show a preference for scattered subclimax types of forests rather than dense climax woods. In winter they gain most of their food from seeds and buds of the conifers, but in summer they are frequently seen on the ground in search of invertebrates or seeds. Pine grosbeaks generally move down to lower elevations in winter, although some apparently remain at high altitudes throughout the seasons. Observations indicate that the birds use conifer seeds very little for food. In summer they are very often seen on the ground feeding on the seed pods of the dog-toothed lily and *Caltha*. In winter they tend to follow along streams feeding upon the buds of willows, alders and birch. Crossbills fed almost exclusively on conifer seeds but occasionally take seeds and some animal matter from the ground.

In summer the food of the chipping sparrow appears to be almost entirely animal. Their young are fed almost exclusively on the larvae and adults of insects. They are also frequently startled from the ground. Chipping sparrows are among the most abundant and conspicuous birds in the mountains in summer. Their nests are almost always placed in conifers, but they frequent aspen woods where there are seedling conifers in which to build the nests. Where no conifers are available they utilize aspens or some of the taller shrubs.

Finally, there is a group of birds that nest in trees or shrubs and gain their food either from these plants or from flying insects in the air surrounding them. They are seldom if ever seen upon the ground except in search of material to build their nests.

Hammond's flycatcher, western flycatcher, western wood pewee, and olive-sided flycatcher and the violet-green swallow, tree swallow and purple martin all utilize trees as nesting sites and feed upon insects caught on the wing. All of these are summer residents, and all except the olive-sided and western flycatchers are confined to aspen forests. Flycatchers build their nests on dead horizontal limbs in most cases, but perch on outside or top twigs watching for food. The swallows

both build in holes in dead or living aspens. Martins also nest in holes in aspens, using the green leaves of the trees to line the nests. These leaves are kept fresh at all times by the continuous addition of new ones.

Another group of birds nest in the trees and gain their food mainly from trunks, branches and twigs. Nearly all of these remain in the forests throughout the year since their food is available at all seasons. These include Natalie's sapsucker, red-naped sapsucker, Rocky Mountain hairy woodpecker, Batchelder's woodpecker, alpine three-toed woodpecker, red-breasted nuthatch, Rocky Mountain nuthatch, mountain chickadee, long-tailed chickadee, and the Rocky Mountain creeper. All of these birds nest in holes in trees and utilize the invertebrate inhabitants of trees and the larger shrubs as food. Both sapsuckers feed to a certain degree on sap of trees and larger shrubs. Nearly all of the trees and larger shrubs both deciduous and evergreen are utilized by these sapsuckers. Certain individual trees appear to be a favored source of food and are visited consistently from year to year. In the main this coaction does not appear to effect the growth of the plant, except where small trees are visited persistently, in which case they eventually become killed or badly distorted.

Some of the species listed above are confined mainly to aspen forests and others to conifers. The alpine three-toed woodpecker appears to be confined to the Upper Montane climax.

There is still another group of birds confined chiefly to the tree layer that gains its food in large part in the form of invertebrates directly from tree foliage or nearby shrubs. This includes the broad-tailed hummingbird, golden-crowned kinglet, ruby-crowned kinglet, Rocky Mountain Audubon's warbler, western warbling vireo and western tanager. The hummingbird obtains most of its food from blossoms of herbs and in this respect differs from the other species. The western tanager eats a good deal more vegetable matter than the others in the form of berries and buds.

All of this last mentioned group are migrants except the kinglets. The latter change their habits in winter and move into the valleys and foothills where there is more ground food available. They also seem to gain considerable food from trunks and branches at that season.

The Pacific nighthawk shows an interesting relationship in that it nests on the ground, rests in trees, and feeds on the wing.

## 3. BIRD POPULATION

(Fig. 9)

Comparative bird populations, arrived at by the cruising method previously described, appear to differ widely from place to place even within a given type of habitat and also show a marked fluctuation throughout the summer months of June through September (Fig. 9). For this reason it is difficult to arrive at a population figure that is representative of any one community. The nesting season which for the majority of montane birds occupies the months of June and the first two or three weeks of July may be taken as a standard, since at that season, populations show the greatest stability. Using this standard it is then possible to analyze the population shifts and migratory movements characteristic of other seasons.

The highest populations during the nesting season (50 per hectare covered) were found in the aspen subclimax. This figure would hold only for mature forests where many nesting sites are available and water is near at hand. General observations where more extended aspen communities of all types occur indicate that the number obtained is high for the community as a whole. The difference between the bird population of the Lower Montane climax (38 per hectare) and the aspen forest is indicative of the subclimatic nature of the latter. The relative high nesting population in the Upper Montane of Mt. Timpanogos is further evidence of its being a subclimax.

It will further be noted from figure 9 that the Upper Montane climax shows the lowest breeding population of any of the communities studied. This would be expected from the extensive and continuous nature of the forests, which conditions are generally not conducive to high bird populations. The Lower Montane climax, on the other hand, shows a relatively high population. As has been previously pointed out, the Lower Montane climax never occurs as extensive and continuous forests in the areas studied, and, therefore, partakes more of the nature of a forest edge, a circumstance which is compatible with higher bird populations.

A general postnesting up-mountain shift in bird populations is quite apparent from both quantitative and general observations. This is brought about by a shifting to higher elevations of species that breed at lower altitudes, and by altitudinal shifts of birds that commonly breed throughout both associations of the montane forest. Indications are that this up-mountain movement is to some extent a daily affair especially on steep mountains such as Timpanogos where higher elevations may be quickly attained with a minimum of linear

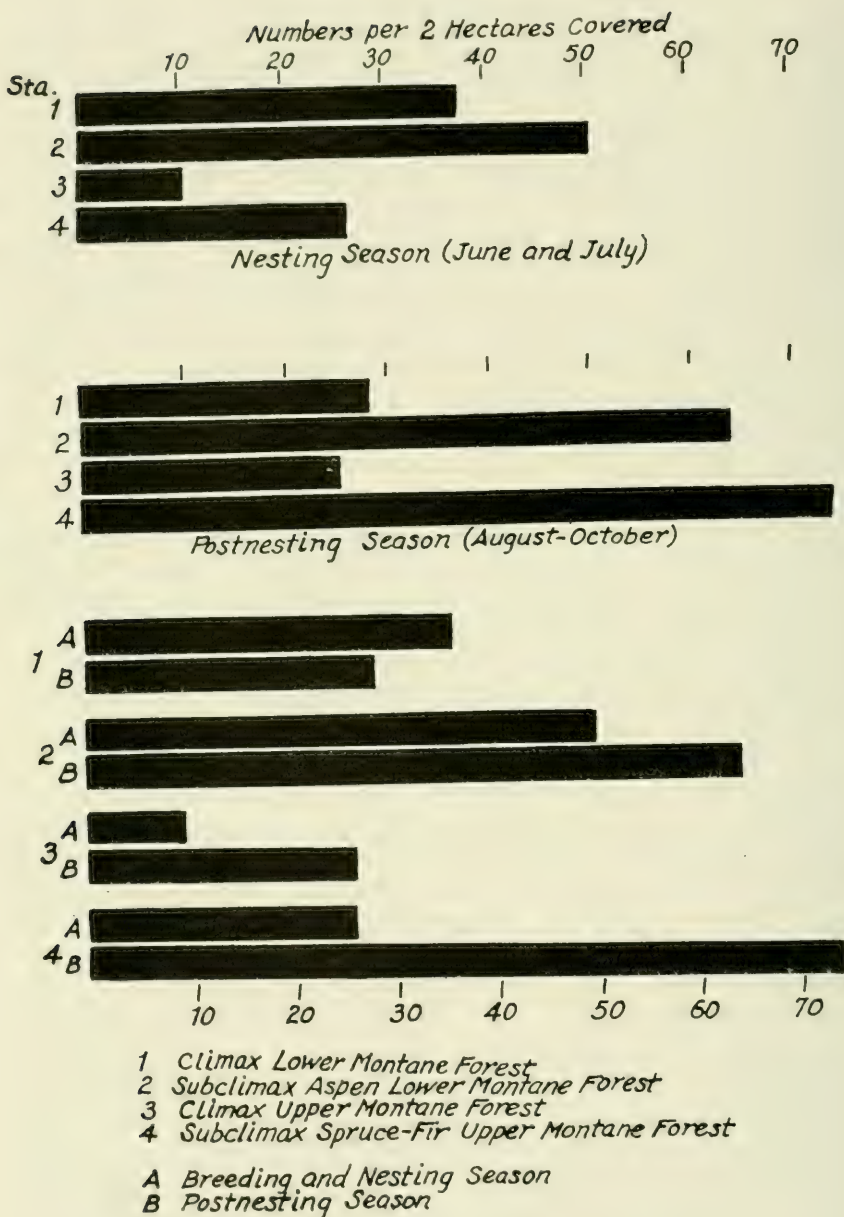


Fig. 9. Relative summer populations of coniferous forest birds as shown by census.



travel. Certain of the birds apparently move into the higher altitudes in early morning and return in the evening to roost at lower levels. These daily flights, associated with the general flocking tendency following the nesting season, are greatly influenced by local or general weather conditions over the mountains. During a stormy period from September 2 to 4, 1940, there were very few birds in the Upper Montane of Timpanogos. Even during breaks in the storm when conditions were conducive to feeding, birds appeared only in small numbers. When the area was again visited on September 10 following the stormy period 77 birds were counted over a two hectare area. General observations made at lower elevations during the same time showed a general reversal of the above condition.

This post-nesting up-drift of bird populations is less marked in the Uinta Mountains (Fig. 9) than it is in the Wasatch, but it is nevertheless evident. The green-tailed towhee, western vesper sparrow, Macgillivray's warbler, western wood pewee, yellow warbler and Brewer's sparrow are the more common species to follow this procedure in both the Wasatch and Uintas. During about 6 weeks of continuous field work in the Upper Montane of the Uintas Hayward (1931) did not observe the Red-shafted flicker until July 26 after which it became common. Concentrations of large numbers of sparrow hawks (Tanner and Hayward 1934, p. 226) have been noted at timber line and above in the La Sal Mountains in late summer.

Explanations of these post-nesting travels as well as other altitudinal shifts are mainly speculative. Undoubtedly many of the factors thought to be contributive to bird migration in general and so copiously discussed in the literature would apply to these shorter altitudinal movements. At first thought it might appear that the search for food is an important item since vegetation at higher levels reaches its peak of succulence after the plants at lower elevations have begun to wither. However, my quantitative samples of invertebrates do not show any general decrease in populations in late summer even at lower elevations but on the contrary often show an increase in the quantity of animal food; and surely there is a greater abundance of seeds and fruits available later in the season.

It should be further pointed out that there is no mass movement of all the birds from one elevation to another, but rather a concentration of populations at higher levels and a gradual thinning toward lower elevations.

From what is known regarding the bird population trends at vari-

ous seasons in the Wasatch and Uinta Mountains area the following summary may be drawn:

1. The winter period, insofar as birds are concerned, extends from about the middle of October to the last week in April. During this time there is a general thinning of populations at higher elevations and a concentration of birds in the chaparral and valley particularly at the mouths of canyons as they open into the valleys and along the stream floodplain. Species remaining in the Montane Forest include mainly those forms that are able to gain their food from tree trunks or branches (woodpeckers, chickadees, etc.) and those that live on exposed fruits or buds. A few predators likewise remain at higher elevations to feed upon active mammals or other birds. Those species that occur at lower elevations in winter are mainly ground feeding forms (see Hayward, 1935) that include migrants from more northern latitudes and also altitudinal migrants. These species depend upon exposed areas where the snow cover is light and generally of short duration, so that an abundance of food is available at all times.

2. A period including the last week in April and extending through May is one of great instability in bird populations. At this time, the more northerly nesting species are moving out, there is an up-mountain movement of local birds to the nesting grounds, and migrants from the south are moving in. These latter species usually arrive first in the valleys and foothills and then gradually drift up the mountains to the nesting grounds.

3. While nesting of some resident species, especially hawks, owls and jays, is carried out during the early spring instability period mentioned above, the great majority of the nesting in the montane forests is carried out during June and the first two or three weeks of July. This is, therefore, the period of greatest stability in populations.

4. The nesting period is followed by the period of up-mountain drift especially in late July, August and early September.

5. The final period in the cycle overlaps somewhat the post-nesting season mentioned above. It extends from about the middle of September to the middle of October. During this time there is a general shifting back and forth from high to low elevations of those species that are ultimately to winter in the foothills and valleys. The degree of this movement depends largely on the state of the weather. Southward migrants are at this time moving out, drifting in from the north, or passing thorough enroute to more southern climates.

## 4. REPTILES AND AMPHIBIANS

Reptiles and amphibians are poorly represented in the montane forests and are apparently of little ecological importance. The smooth green snake (*Opheodrys vernalis blanchardi*) seems to be confined to the Lower Montane Association and some of its adjacent associates. It is so rarely seen that the writer has been able to gain little information as to its habits. It is usually seen on the lower branches of conifers in summer and hibernates under rocks, mostly outside of the forest in winter. The rubber boa (*Charina bottae*) seems to be confined more to seral stages but its distribution is not well known. The common water snake (*Thamnophis ordinoides vagrans*) which is also found in the valleys, is common near streams and often hunts some distance out into the forests. It extends up into the Upper Montane but is more common at lower elevations.

The amphibian, *Pseudacris nigrita triseriata*, is found near lakes in the montane forests and will often extend out into the climax in wet summers where it lives under logs and rocks. The tiger salamander (*Ambystoma tigrinum nebulosum*) is mainly aquatic but wanders out on land occasionally. The common *Rana pipiens* is also found about ponds in certain places in the Wasatch but it is not common where this study was made. *Bufo boreas boreas* is common about streams and springs at all elevations in the montane forests. Distribution of Utah Amphibia according to the life zone concept has been shown by Tanner (1931, pl. IX).

## VI. SUCCESSION IN THE MONTANE FORESTS

Time did not permit the detailed study of the seral stages leading up to the climax and subclimax forests, but general observations concerning the more common plants and larger animals were made. It may be said in general that the climaxes develop from both hydroseres and xeroseres in common with conditions throughout the country as a whole.

A portion of the stream side hydrosere of the Lower Montane Forest on Mt. Timpanogos was studied by Harris (1926), but included only the plants. This sere develops from cold streams or springs in deep-cut canyons. Such streams are bordered by thickets of *Salix*, birch (*Betula fontinalis*), and dogwood (*Cornus stolonifera*). The narrow floodplain is vegetated with a variety of herbaceous plants and a mixture of both low and high altitude trees. The Engelmann spruce, a climax tree of the Upper Montane, here mingles with Blue Spruce (*Picea pungens*) as well as the cottonwood (*Populus angustifolia*) (Fig. 5 E) which is characteristic of the floodplains of the

valley floor. Aspen may also be found in this mixture. From this floodplain stage the sere generally passes directly into the climax forest or the aspen subclimax, whichever happens to be bordering the stream.

All of the major influent animals range freely into the early stages of the sere, but such animals as the navigator shrew (*Sorex palustris navigator*) and the big-footed meadow mouse seem to be confined strictly to the streamside. The Utah jumping mouse, cantankerous meadow mouse and common *Peromyscus* appear to reach their greatest numbers in the early stages of the sere; although they extend more or less out into the climax forests as well.

The beaver in certain localities is found in the early hydrosere, building dams across the streams and utilizing the willows, cottonwoods, aspens and to a lesser degree conifers in the construction of the dams or as food.

The dipper (*Cinclus mexicanus unicolor*) is confined entirely to the streams and the spotted sandpiper occurs on streambanks in some localities.

In general, the Lower Montane Forests are not so extensively influenced by snowslides as the higher forests on Mt. Timpanogos. However, at certain points where snow is able to collect above the forests, snowslide paths (Fig. 2) or temporary seepage from persistent snowbanks retard the development of the climax. Such places are covered with dense growths of shrubs made up essentially of the same species that form the undergrowth in climax forests. These thickets have not been extensively studied, but a few of the chaparral birds, especially Virginia's warbler and the green-tailed towhee are known to breed there.

On Mt. Timpanogos, the replacement of aspen forests by conifers is well illustrated in a number of places (Figs. 3, 4, 5). This appears to be going on in at least three different ways. In aspen forests that are far removed from conifers and at lower elevations the principal tree found in the undergrowth is the white fir (*Abies concolor*). In some areas these trees appear to be making fairly good progress in the development of a climax, but in other localities it is a slow and difficult process due to the coactions of the porcupine, deer, snowshoe rabbit, and sapsucker already mentioned. These conditions probably account for the old aspen forests and the slow return of the climax where the replacement is by the white fir.

A second mode of replacement found in higher altitudes near the upper elevation limits of the aspen, is being accomplished by the alpine fir (*Abies lasiocarpa*). This conifer occurs in small groves of almost



pure stands of mature trees, usually on steep slopes of canyons and gullies and from these centers invades the aspen forests in all directions. These trees are also attacked by the deer and snowshoe rabbit but not so often by the porcupine. In general they seem to be able to cope better with these conditions than the white fir and the process of replacement is more rapid.

The third type of invasion which appears to be more rapid and permanent, occurs where the aspen forests border the climax Lower Montane. The seeds of the Douglas Fir are winged and carried by the wind, so that this type of invasion usually progresses toward the east.

The rate at which coniferous forest animals follow the invading trees appears to vary considerably. Certain birds, notably the red-breasted nuthatch and purple finch follow closely the first conifers as soon as they reach an average size. This is also true of the snowshoe rabbit. However, the red squirrel does not become established until a coniferous forest at least a half hectare in area is reached.

Developmental stages in the Upper Montane of the Uinta Mountains are well marked. The hydrosere proceed from small streams and from the borders of lakes and ponds (Fig. 5 C). Running through the forests are many small streams from a foot to several feet wide which empty ultimately into lakes or ponds. These streams are fringed with a narrow border of grasses, sedges, and mosses; and next to this is a band of low shrubs composed mostly of *Vaccinium occidentale* and *Salix planifolia*. In addition a number of hydric herbs such as *Trollius albiflorus* and *Caltha leptosepala* are to be found here. Sedges and grasses are also abundant. These seral stages occupy a narrow border only a few feet wide and pass directly into the climax or sub-climax forests.

A number of small mammals appear to be confined chiefly or entirely to the wet borders of these streams. These animals include the navigator shrew, big-footed meadow mouse, and dwarf meadow mouse (*Microtus montanus nanus*).

Glaciation in the past has resulted in the formation of a great many lakes and ponds which occupy open spaces in the midst of the forests. These bodies of water are normally surrounded by meadows of varying extent and in some places have been completely filled up so as to leave only the meadows. The succession from these bodies of water varies somewhat according to the nature of the shore; i. e., whether it is boggy or rocky. Some observations were made at Lily and Diamond Lakes which give some indication of the succession processes of a typical boggy lake.

Such lakes are generally acid with a pH of about 4 (Cottam, 1930). A number of typically acid tolerant plants grow in the water or at the water's edge. These include *Sphagnum* moss, *Isoetes* (a plant closely allied to the ferns), and the yellow pond lily (*Nymphaea polysepala*). The *Sphagnum* especially tends to grow out over the water so as to form typical springy margins. The meadows immediately surrounding the lakes are wet and boggy. Some of the common plants found there are *Ligusticum tenuifolium*, *Gentiana calycosa*, *Swertia scopulina*, *Bistorta bistortoides*, *Caltha leptosepala*, *Pedicularis groenlandica*, *Trisetum wolfii*, *Phleum alpinum*, *Deschampsia caespitosa*, *Clamagrostis canadensis* and a number of species of *Carex*.

These meadows continue to higher and better drained ground where the most common plant species are *Trifolium parryi*, *Ranunculus eschscholtzii*, *Potentilla glaucophylla*, *Juncus halii*, *Viola nephrophylla*, *Erythronium parviflorum*, and *Trisetum spicatum*.

The first conifer to invade these meadows is the lodgepole pine, which usually appears as a fringe bordering the meadow and next to the climax trees. The tolerance of this tree to more soil moisture and greater acidity, as well as its requirements for more light probably accounts for this condition. It is later apparently encroached upon by the climax trees. Being intolerant of shade, it is gradually crowded out.

Only general observations can be made at this time on the animals of this hydrosere. The Rocky Mountain muskrat (*Ondatra zibethica osoyoosensis*) lives in the lakes and makes its runways in the bank. It feeds upon the stems of the water lily and also upon sedges which grow next to the water. There is often a narrow border of these clipped clean next to the water. The beaver is more often found along the streams of the Lower Montane but it occasionally occurs in the lakes of Upper Montane in the Uintas. In such places it feeds on conifers adjacent to the water and also dwarf willows, and water lilies. It builds houses of conifer branches and sphagnum. The Uinta pocket gopher is almost exclusively confined to the dryer portions of the meadows. *Citellus armatus*, the Uinta ground squirrel, lives in still higher ground in the fringe of lodgepole pine, but feeds a great deal in the meadows. The small amphibian *Pseudacris triseriata* breeds in the ponds and lakes, and adults occur around the borders. In wet seasons they also move out into the climax forests.

## VII. THE ALPINE MEADOW

## A. GENERAL FEATURES

(Fig. 12)

The alpine meadows of Mt. Timpanogos are found in cirques at elevations generally above 10,000 feet. They appear to represent the climax of the alpine communities and are best developed in rather flat areas where soil has accumulated over the rock substratum to a depth of several inches and where the ground is exposed for from three to five months of the year. These meadows are not continuous over large areas but are comprised of small patches from a few square yards to several acres in extent. These areas of alpine climax are separated from one another by boulder fields, moraines, and rocky outcroppings in various stages of succession.

The general aspect of the meadow is one of low-growing vegetation from one to four inches high, with some of the more succulent herbs and taller grasses forming a higher stratum late in the growing season. Dominant plants are sedges, with grasses and a variety of herbs of secondary importance. The vegetation as a whole consists of a number of alpine plants and northern species mixed with species from lower elevations. Dominant sedges include *Carex festivella*, also common at lower elevations and a number of other *Carex* as yet undetermined. The more important grasses include: *Poa reflexa*, *Poa alpina*, *Poa secunda*, *Phleum alpinum*, *Trisetum spicatum*, and *Agropyron pauciflorum*. Herbs found in greatest abundance are a parsnip, *Ligusticum filicinum*, and the common bistort, *Bistorta bistortoides*. A number of species of the rose family are also found, including *Potentilla filipes*, *Sibbaldia procumbens*, and *Argentina anserina*.

In general, Cox's (1933) description of the alpine flora of James Peak, Colorado, fits the situation found on Mt. Timpanogos although many of the species are not identical. However, that writer designates *Elyna bellardi* as one of the climax dominants. This plant is rare in Utah (Tidestrom, 1925, p. 102 and Graham, 1937, p. 147) and, as far as the writer knows, does not occur on Mt. Timpanogos. It is known to occur in the Swiss Alps also.

In any consideration of the ecology of a community such as the alpine meadow it is convenient to regard the vegetation, together with its invertebrate population, as a biotic matrix into which the larger animals permeate and upon which they depend largely for sustenance and protection. Insofar as the larger animals themselves effect this matrix directly through coaction or indirectly through reaction they

may be considered as influents of various categories (Clements and Shelford, 1939, p. 241).

In the alpine meadow as it occurs on Mt. Timpanogos, ground layer and herb layer societies may be recognized. The ground layer consists of sod formed by the tough roots of the vegetation as well as protected places under stones, piles of animal droppings and plant debris.

Invertebrate inhabitants of the ground layer society consist of a number of species that live under the protection of the scanty cover provided; while a few, mainly larvae, burrow into the sod itself. Those that creep over the surface of the ground but feed and seek protection mainly in the herb layer are not included in this community. Certain species, notably ants, nest in the ground layer but feed largely in the vegetation. These may be considered as permeants in the biotic matrix.

Table III

Average estival populations of invertebrates living under the protection of rocks, animal scat, and plant debris of the climax alpine meadow. The list includes only those animals identified at least as far as the genus. Numbers represent individuals per unit area of ground exposed by turning over protective objects. The figures, therefore, are of comparative value only.\*

Hemiptera	
<i>Geocoris bullatus</i> (Say) .....	12
Coleoptera	
Carabidae	
<i>Harpalus carbonatus</i> Lec. ....	6
<i>Amara</i> sp. ....	2
<i>Amara obesa</i> (Say) .....	1
Curculionidae	
<i>Sitona</i> sp. ....	8
<i>Panscopus schwarzi</i> Buch. ....	2
Elateridae	
<i>Ludius aereipennis</i> (Kby.) ....	2
<i>Hypnoidus lucidulus</i> (Mann.) ....	4
<i>Hypnoidus lecontei hirsutus</i> Van. D. ....	1
Scarabaeidae	
<i>Aegialia</i> (near) <i>lacustris</i> Lec. ....	1
Chilopoda	
<i>Lophobius collium</i> (Ch.) ....	3
Araneida	
<i>Pardosa indagatrix</i> Thorell. ....	3

\*The ant species *Formica fusca gelida* and *Lasius niger neoniger* are also found in colonies under stones.



Table IV

Average summer populations of invertebrates on the herb layer of climax alpine meadows, Mt. Timpanogos. Numbers represent animals taken in 500 sweeps with a net having a diameter of 30 cm. Samples of 50 sweeps each were taken at about four week intervals during the June-September period of 1938, 1939 and 1940. Only those forms determined at least as far as genus are included:

Homoptera	
<i>Dikraneura carneola</i> (Stal.)	382
<i>Deltocephalus dorsti</i> Oman	20
<i>Laczicephalus debilis</i> (Uhl.)	31
<i>Eutettix tenellus</i> (Baker)	1
<i>Macrosteles dahlbomi</i> (Zett.)	1
<i>Thamnotettix germinatus</i>	1
<i>Aphalara simila</i> Caldwl.	1
<i>Trioxa</i>	6
Hemiptera	
<i>Nabis alternatus</i> Parsh	4
<i>Deracocoris brevis piceatus</i> Knight	1
<i>Geocoris bullatus</i> (Say)	8
<i>Stenodema virens</i> (L.)	2
<i>Nysius grandis</i> Baker	1
<i>Nysius californicus</i> (Stal.)	1
Coleoptera	
<i>Coccinella transversoguttata</i> Fald.	2
<i>Hippodamia complex</i> Csy.	2
<i>Hippodamia parenthesis</i> (Say)	1
<i>Hippodamia convergens</i>	1
Orthoptera	
<i>Melanoplus</i> (Nymphs)	13
<i>Melanoplus infantilis</i> Scudder	2
Diptera	
<i>Lasiops septentrionalis</i> (Stein)	1
<i>Hydrellia griseola</i> (Fall.)	1
<i>Philygria debilis</i> Loew	1
<i>Tomosvaryella utahensis</i> Hardy	1
<i>Voria ruralis</i> (Fall.)	1
<i>Sarcophaga l'herminieri</i> R. D.	1
<i>Trupanea radifera</i> Cog.	2
<i>Tephritis clathreta</i> Lw.	3
<i>Chlorops stigmata</i>	1
Hymenoptera	
<i>Halictus</i>	2
<i>Formica fusca</i> Linn.	5
<i>Lasius niger</i> Linn.	2
<i>Chelonus</i>	2

<i>Orgilus</i> .....	1
<i>Podalonia luctuosa</i> (Sm.) .....	1
<i>Bremus occidentalis</i> (Greene) .....	1
<i>Sagaritis strigosus</i> Vier. ....	1
<i>Olesicampe</i> .....	1
Araneida	
<i>Metaphidippus nigromaculatus</i> .....	1

The invertebrate population in exposed places shows an average of about 40 animals per square meter for the summer. This population in the soil layer seems to reach its maximum in August when there is an average of about 100 animals per square meter. About 40% of this maximum population consists of mites (Acarina) of several species as yet undetermined. Ground-dwelling beetles occur to the extent of about 23% while ants (Formicidae) comprise about 14% of the population. The common and widespread burrowing bug, *Geocoris bullatus* (Say) makes up about 20% of the ground population in summer. This species is also common in the herb layer. Sampling of the ground layer in exposed places brought variable results. In some of the samples no animals whatever could be found while in others as many as 150 occurred per square meter.

Most of the invertebrates of the ground layer are to be found under the protection of rocks, piles of animal droppings and debris. Numbers of species found in such places are shown in Table III. Occasional ant colonies are found under stones but no attempt was made to arrive at the numbers of individuals in these colonies.

The more common herbs of the alpine meadow have already been listed. This layer society shows a decided difference insofar as the invertebrate animals are concerned. Populations of the invertebrates identified from samples are shown in Table IV. In contrast to the ground layer, about 84% of the population consists of leafhoppers, mostly of one species (*Dikraneura carneola*). Hemiptera comprise about 5% and Diptera 4%. The proportional population of Diptera is much lower than in the arctic tundra where it may compose nearly 100% of the invertebrate population (Shelford and Twomey, 1941, p. 65). Certain of the larger and more active insects, notably Orthoptera and Lepidoptera, are not readily taken in ordinary samples but are, nevertheless, important constituents of the biotic matrix. Grasshoppers become especially abundant in August and September and constitute an important item of food for visiting birds.

Butterflies constitute a conspicuous feature of the alpine invertebrate fauna, flying in large numbers over the alpine meadows but espe-

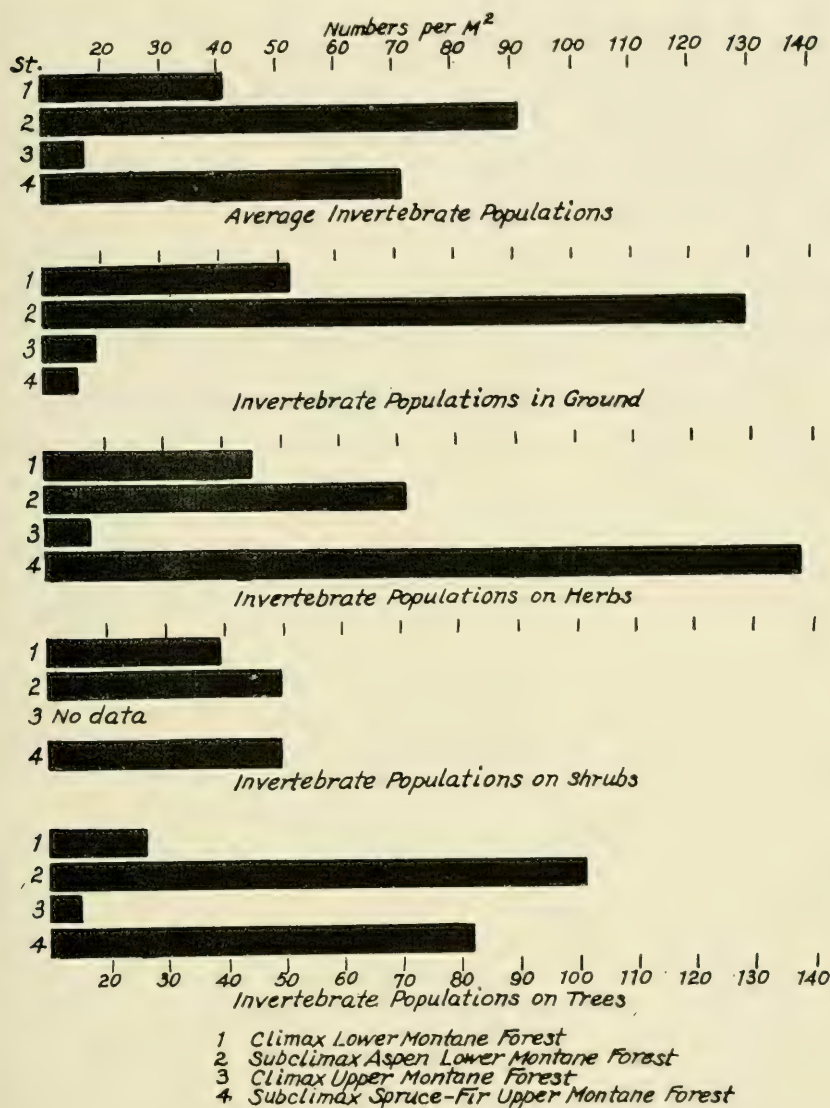


Fig. 10. Relative populations of invertebrates in the several layer communities of the coniferous forests.

cially over the seral stages where masses of bright colored flowers are in blossom in June and July. About 24 species have been recorded from these communities. *Parnassius clodius* is apparently confined to the alpine and is one of the more common species on Mt. Timpanogos.

Other common species include *Nymphalis californica*, *Euphydryas chalcedona*, *Argynnis utahensis*, *Argynnis nevadensis*, *Vanessa cardui* and *Vanessa carye*.

#### B. INFLUENTS

In the alpine communities of Mt. Timpanogos, the golden-mantled marmot (*Marmota flaviventris mosophora*) is one of the more important rodents. This animal reaches its greatest abundance in the alpine, although it is found in rocky places at all elevations on the mountain. In the alpine, it feeds mainly on the open meadows but lives mostly in loose rock piles or along rocky ridges. Not infrequently, however, its burrows are found on the climax meadows. As many as six of these animals have been seen feeding at one time on a half acre of alpine meadow. They emerge from hibernation in May or June, often by burrowing up through the snow, and remain active until about the middle of October.

Smaller mammals found on the alpine of Mt. Timpanogos likewise consist of those that are found at lower elevations. Strangely enough the Uinta ground squirrel (*Citellus armatus*) reaches its greatest abundance in the alpine of Mt. Timpanogos but is almost entirely absent from similar elevations in the Uinta Mountains. There were about twice as many burrows (63 per hectare) on the alpine meadow as there were at a station in the aspen forest subclimax on Mt. Timpanogos.

The period of activity of the ground squirrel varies greatly from year to year, depending upon the amount of snow deposit. On June 28, 1937 about 65% of the ground was covered with snow and there were no *Citellus* in evidence. On June 26, 1940 most of the snow was gone and there was considerable growth of vegetation. At that time adult squirrels were abundant although no young were present. When the same area was visited on July 14, 1941 there was again much snow and squirrels were very rare. On that date only 4 animals were seen in 5 hours of field work. It appears evident that the period of squirrel activity may be as much as two months shorter in the alpine than it is at the lower elevation range of the same species. Whether this condition means a longer hibernation period, or whether this high summer population consists in part of emigrants from lower elevations are questions that cannot at present be answered.

The activities of the ground squirrel appear to coincide with the prevalence of succulent vegetation. Their food consists mainly of forbes rather than sedges and grasses. In early spring they feed upon



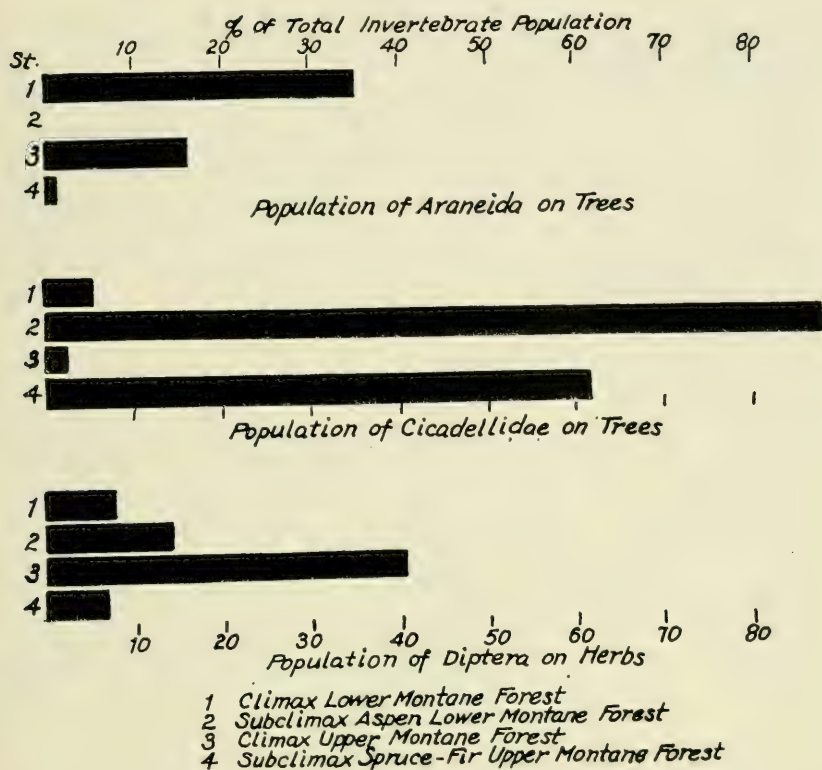


Fig. 11. Population of Araneida, Cicadellidae and Diptera in certain layer communities of the coniferous forests.

the tender tips of these plants as they emerge from the ground, or they may even dig for them. Later, when the plants are taller, they are pulled down and the terminal portions are eaten. The squirrels appear to feed more or less indiscriminately upon whatever plants are most available.

Hibernation takes place about the first of September, which is two to three weeks later than it does at an elevation of 7,000 feet. There are, therefore, about 8 to 10 weeks available for the activity of the ground squirrel in the alpine community.

It should be pointed out that the presence of large numbers of ground squirrels in the alpine areas of Mt. Timpanogos is not a common feature of alpine communities of the Rocky mountains area generally (Howell, 1938, pp. 10-11, and Davis, 1939, p. 172). Due to the steepness of the mountain and the abrupt transition between alpine

meadows and coniferous forests, together with the fact that a movement of animals from one to the other would involve relatively little travel, the possibility is great that many of the animals found in alpine meadows on Mt. Timpanogos, in summer shift in from lower elevations, and may not represent animals that have hibernated at these high altitudes. Such an explanation would preclude the necessity for the animals to remain in hibernation approximately ten months of the year, which would be the case if they were permanent residents of the alpine. However, such a prolonged hibernation may not be impossible, and direct evidence for an up-mountain shift in squirrel population is lacking.

The pocket gopher (*Thomomys talpoides moorei*) is also very common in the alpine meadow. Counts of workings indicate that they occur to the extent of at least 18 animals per hectare. Winter activities are very conspicuous when the snow first leaves the ground in early summer. These winter activities occur in the form of shallow and tortuous furrows on the surface of the ground or the familiar earthen cores made by plugging soil into the snow burrows. In early summer the damp earth mounds commonly thrown up by these animals are never as abundant as they are in late summer and autumn. This, together with the fact that green vegetation is more frequently found in the cheek pouches at the early season, indicates that the gophers may feed more extensively on surface vegetation in early summer. At this season, gophers are occasionally caught in surface traps many yards from the nearest burrow, and the animals are often taken by predatory birds, especially owls, at this season.

Davis (1939, pp. 241-242) and Marshall (1941, p. 196) have recently described the burrowing habits of *Thomomys*. Grinnell (1923) outlines the beneficial effect of this reaction to general soil conditions. On Mt. Timpanogos, the effect particularly of the winter activities are strikingly evident immediately after the ground is exposed by the melting snow. At such times as much as 90% of the surface of the ground may be covered by soil turned up by gopher activity and it is estimated that 50% of the whole alpine meadow is effected in this way. A few beating rainstorms obliterate the evidence of the activity and the alpine vegetation comes up through the loose soil. Extensive as this activity is, it does not seem to influence noticeably the sod forming capacity of the climax dominants.

The Uinta pika (*Ochotona principis uinta*) reaches its greatest abundance in alpine regions although it is found consistently in suitable habitats throughout the montane forests. This animal lives in crevices

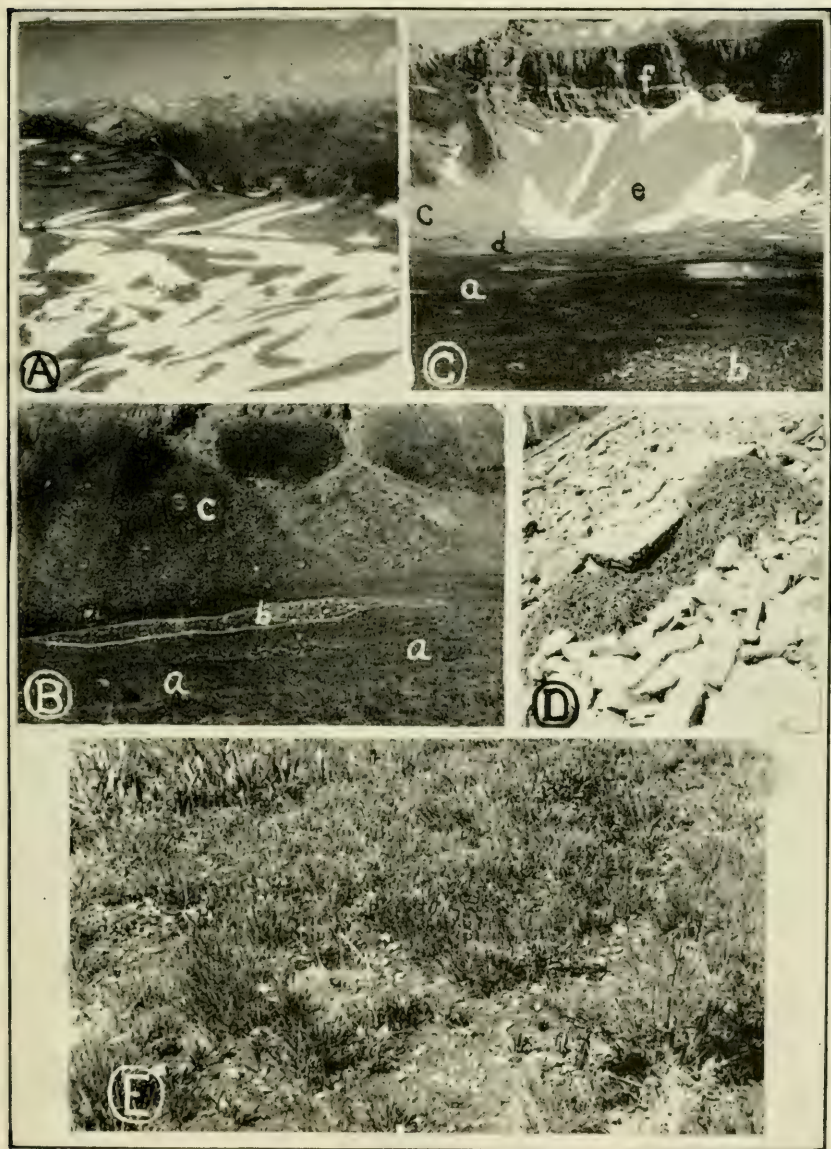


Fig. 12. A, General view of Alpine meadow, American Fork Cirque, Mt. Timpanogos, photographed July 14, 1941. B, Alpine meadow: (a) climax, (b) old moraine, (c) old talus slope partly stabilized. C, Alpine meadow and adjoining cliff: (a) climax, (b) old moraine (c) old talus slope, (d) recent moraine, (e) active talus slope, (f) barren cliffs. D, "Haystack" of pika in typical habitat. E, Vegetation of alpine meadow climax.



in loose rock piles and gains most of its food from early seral stages; however, if its living quarters are near the climax meadow, it obtains a portion of its food there.

As is well known, the pika stores food for winter use in the form of miniature "haystacks" (Fig. 12 D). The gathering of this material begins about the middle of June, but it is most intensive in August and September. The piles are frequently stored under the protection of rocks, but they are often quite exposed. In the latter case they are rounded so as to shed a good deal of rain. Material is added to the piles so gradually that it usually has time to dry thoroughly before it is covered; thus the hay is generally well cured throughout.

Plants used in constructing these piles vary a great deal and depend upon whatever species are near at hand. There seems to be little food preference in this case. In general, however, the foods found in these piles are the most succulent herbs rather than grasses and sedges. The writer has no record of any shrub being used. Plants that have been identified from the piles include *Mertensia leonardi*, *Cirsium lanccolatum*, *Frasera speciosa*, *Aquilegia caerulea*, *Ranunculus adoneus*, *Erigeron* sp., *Zygadenus elegans*, *Bistorta bistortoides*, and *Ligusticum flicinum*.

The golden mantled ground squirrel (*Citellus lateralis castanurus*) is occasionally found in the alpine of Mt. Timpanogos. It is confined almost entirely to rock piles, occupying much the same habitat as the pika. Only rarely is it seen on the climax meadows. It is not as common on Mt. Timpanogos as it is in some other parts of the Wasatch, and the writer has had little opportunity to study its habits.

The only mouse that has been found on the alpine meadows of Mt. Timpanogos is *Peromyscus maniculatus* ssp. It formed a hundred per cent of the small mammal population trapped on plots on these meadows. Furthermore, the mammal seems to occur there only in late summer and autumn. Three different years of trapping in June on the climax meadows failed to reveal any of these animals, but they were always present later in the season. In the autumn of 1939 there was a population of about 46 per hectare trapped, while in 1940 there were 32 per hectare trapped.

It is the writer's belief that these animals spread out on the alpine from the surrounding coniferous forests in summer and then are driven back or killed off in late autumn or winter because of the lack of suitable cover. Since these mice are active throughout the year, the probability of survival, on the alpine meadow where all food is covered by many feet of snow, would indeed be small, although some burrowing



in the snow may occur. Furthermore, there would be practically no cover available during the winter season. In summer, deserted holes of the burrowing rodents afford suitable hiding places for the mice during the daytime.

Cary (1911) records the occurrence of *Microtus* on the alpine meadows of the Colorado Rockies, but the writer has no evidence of their presence on the alpine of Mt. Timpanogos. The Rocky Mountain phenacomys (*Phenacomys intermedius intermedius*), Gale Red-backed Mouse (*Clethrionomys gapperi galei*), cantankerous meadow mouse (*Microtus mordax mordax*), as well as two chipmunks (*Eutamias quadrivittatus umbrinus* and *E. minimus consobrinus*) inhabit the krumholz ecotone adjacent to the alpine, but apparently they do not venture far from the cover of these stunted conifers.

The larger influent animals of the alpine meadow consist entirely of species that visit it from lower elevations and it is probable that none of them remain active there throughout the year. Early records indicate that the mountain sheep (*Ovis canadensis canadensis*) formerly occurred on Mt. Timpanogos and undoubtedly fed upon the alpine meadows; however, judging from the present habits of this animal, they were probably not confined to these communities and none is to be found on Mt. Timpanogos at the present time.

The mule deer (*Odocoileus hemionus macrotis*) is the only large ungulate that regularly visits the alpine meadow although the wapiti (*Cervus canadensis canadensis*) re-introduced on Mt. Timpanogos in 1925, is rarely seen there. The deer is found on the alpine communities from June until October. They, or their signs, have been noted out on the meadows at least a mile from the nearest vegetation cover. Herds of four or five animals or single individuals are frequently seen feeding far out on the meadows in the afternoon or early evening. Most of the feeding, however, is apparently done at night and the animals move into the cover of the Upper Montane Forests in the daytime. Observations indicate that the food is mostly the more succulent forbes rather than the grasses and sedges, although the animals feed indiscriminately in seral stages and climax wherever food is available.

Larger predatory mammals are so reduced in numbers on Mt. Timpanogos that it is difficult to ascertain their former relationship to these communities. The Great Basin coyote (*Canis latrans lestes*) visits the alpine both in summer and winter. The badger (*Taxidea taxus* ssp.) feeds there upon pocket gophers and ground squirrels. Areas of several square yards are frequently found dug by these ani-

imals. A skull of the Great Basin striped skunk (*Mephitis occidentalis major*) was found on the alpine meadow, but this probably was carried there by a predator. Remains of the porcupine (*Erethizon epixanthum epixanthum*) are occasionally found, although this animal is primarily confined to the montane forests.

The Nevada weasel (*Mustela frenata nevadensis*) is the most common of the small predators. It has been seen in all of the xeroseral stages and climax but is more often encountered in the loose rock piles where it apparently feeds to a large extent upon the pika. Long (1938) has observed this habit in the Colorado Rockies.

A conspicuous feature of the alpine meadow on Mt. Timpanogos is the low population of birds, particularly during the breeding season. During the years that a census was taken it was estimated that there was not more than one pair of nesting birds per 10 hectares of area. This is in contrast to an estimated 25 birds per hectare in adjoining coniferous forests during the same period.

The Rocky Mountain pipit (*Anthus rubescens alticola*) is the most characteristic bird of the alpine meadows. It is not confined to the alpine, however, but breeds also in meadow stages of the Upper Montane Forest. Its nests are constructed in depressions with the rim level with the surface (Hayward, 1941). These birds work their way down the mountains in August and September and are found in the valley grasslands in winter.

The black leucosticte (*Leucosticte atrata*) is seemingly confined to the alpine in summer. However, it is seen mostly in early xeroseral stages in rock piles and among cliffs. It also prefers the vicinity of snowbanks and is found only rarely upon the climax meadows. In winter most of the birds move down the mountain and live in the foothills in company with other species from the north.

No species of ptarmigan is found on Mt. Timpanogos.

Rock wrens (*Salpinctes obsoletus obsoletus*) are occasionally found nesting in loose rock piles. They occur, however, at all elevations where suitable nesting places are available and are not at all confined to the alpine.

In late summer and autumn, flocks of small birds often visit the alpine meadows in search of food. The most common of these casual visitants are the mountain bluebird, vesper sparrow, Brewer's sparrow, and western chipping sparrow. Most of the large predatory birds common in the general vicinity may also use the alpine communities for feeding purposes. These include the golden eagle, American

goshawk, Cooper's hawk, sharp-shinned hawk, prairie falcon, western red-tailed hawk, marsh hawk, and Montana horned owl.

### C. SUCCESSION

Succession in the alpine region has not been thoroughly studied on Mt. Timpanogos, so that general features only may be considered at this time. It appears, however, that there are at least two hydroseres and two or three separate xeroseres represented.

Where swift-running streams occur over rocks, *Mertensia leonardi* forms dense growths near the water. If the streams occur in flat areas where the soil has accumulated to greater depth the marsh marigold (*Caltha leptosepala*) is the predominant plant, with a number of grasses and sedges also present. The invertebrates of these more hydric stages have not been studied, but most of the vertebrates common to the alpine in general visit these stages in search of food and water. None, however, is particularly confined to it.

Xeroseres may develop either from exposed rock, glacial moraines, or talus slopes of loose rock. Loose rock piles formed as terminal glacial moraines or at the bases of activity eroding cliffs are the most conspicuous of the early stages. This habitat also extends well down into the montane forests, carrying with it its characteristic animals.

The role of the pika in preparing the early loose rock stage for the successional stages that are to follow is interesting to contemplate, although the writer has not been able to gather much direct evidence of its importance. It would appear that the storage piles are almost completely used up during the winter months; but the droppings of the animals as well as inedible parts of the plants, concentrated as they are in definite places, may, in the course of years amount to a considerable deposit in the crevices of the rocks. Should such dwelling places be abandoned it is not difficult to conceive of the pioneer vegetation getting started in such places. The seeding of such areas could easily be accomplished through the agency of such animals as birds and squirrels. The latter especially are known to feed upon the fruits of *Ribes cereum* which is often one of the earlier plants to appear on the rockslides.

Seral stages from loose rock piles to climax meadows were not studied extensively by the writer, but it is evident that the process is extremely slow. This is due to the fact that in many places rapidly eroding cliffs are continuously adding new rocks to these slopes, and the short season of plant growth makes the accumulation of soil, even in areas of relative stability, extremely slow. Many of the talus slopes

are buried under several feet of snow for 10 or 11 months of the year and some are permanently covered. Thus in contrast to succession in sand dunes or ponds in temperate climates, where progress may be recorded in terms of decades or even less, here the process is a matter of centuries or millenia.

In the case of talus slopes and glacial moraines, some of the large pioneer plants are *Ribes cercum*, *Potentilla crinita*, *Frasera speciosa*, *Cirsium lanceolatum*, in dry places. Where there is more moisture such species as *Primula parryi* and *Lupinus alpestris*, are the first of the larger plants to appear.

When the moraines become older, they form rocky knolls with a sparse amount of soil among the rocks. It is in this stage that the brilliant array of alpine flowers is most in evidence with low yet large blossomed flowers in great profusion especially in July. The following plants are most conspicuous in this community: *Festuca kingii*, *Synthyrysus pinnatifida*, *Castelleja viscida*, *Cogswellia triternata*, *Ivesia gordonii*, *Potentilla crinita*, *Phlox multiflora*, *Dasiophora fruticosa*, *Silene acaulis*, *Clematis pseudoalpina*, *Senecio atratus*, *Potentilla glandulosa arizonica*, *Erigeron ursinus*, *Lesquerella utahensis*, *Eriogonum umbellatum*, *Pentstemon cyanthus*, and *Pentstemon humilis breviflorus*.

Associated with the alpine flora of these older moraines are considerable numbers of the larger and more conspicuous insects, especially brightly colored butterflies and bumblebees. A number of the species of butterflies have already been listed. The more common species of bumblebees include: *Psithyrus insularis*, *P. suckleyi*, *Bremus flavifrons*, *B. centralis*, *B. appositus*, *B. rufocinctus*, *B. occidentalis*, *B. sylvicola*, *B. flavifrons*, and *B. bifarius*.

Especially on north-facing slopes of these old moraines there are dense mats of the low-growing willow (*Salix saxi-montana*) which grow almost to the exclusion of all other plants.

The distributional relationships of the animals in the several seres discussed above have not been thoroughly studied. However, it may be said that the pika, golden-mantled ground squirrel, marmot, rock wren and leucosticte inhabit the earlier stages of the xeroseres; while the pocket gopher, badger and pipit are more confined to the climax. The remainder of the vertebrates appear to roam at will over all the stages that supply food and protection.

On Mt. Timpanogos, a large proportion of the alpine area consists of sheer cliffs of almost barren, solid rock. The only vegetation on such areas is lichens and mosses. Such places are usually extremely



xeric and without even snow cover are exposed to all of the extremes of weather.

No mammals frequent these cliffs except a few marmots along ledges and some bats that live in crevices. The golden eagle and possible other hawks nest on inaccessible ledges and the cliff swallow and white-throated swift build their nests in crevices.

#### D. DISCUSSION

The proper placement and classification of the alpine communities, particularly in the more southern ranges of the West, under the biome concept as set forth by Clements and Shelford (1939), and Phillips (1931) and summarized by Carpenter (1939, pp. 75-89) present certain difficulties under our present state of knowledge.

Relationships of these communities to the far northern tundra have long been assumed and referred to many times. Such terms as "Arctic Alpine" employed by Merriam (1898) and "Petran Tundra" used by Weaver and Clements (1938, p. 485) assume these relationships. However, the older term "Alpine Meadow" employed also by Clements (1920) is here used for the climax since the total community aspect resembles very little the northern tundra, and the implication of a close relationship by usage of the terms "tundra" and "arctic" seems misleading.

The alpine communities as they are found on Mt. Timpanogos are not altogether typical of such communities as they are found in western mountains generally, due to a considerable influence of flora and fauna from lower elevations; however, they present enough of the alpine conditions to place them definitely in that category and many of their properties apply to alpine communities in general.

Alpine meadows and their adjoining seral communities of this study appear to have certain ecological qualities in common with the northern tundra: (1) treelessness, (2) low and stunted vegetation, (3) short season of biotic activity associated with some climatic resemblances, and (4) a number of species of plants and a few animals also common to the northern tundra.

On the other hand the alpine communities differ from the arctic tundra in a number of important respects:

1. The terrain in the alpine is generally more rugged and unstable, giving little opportunity for the climax to develop except in very small areas. The general aspect is insular with small widely isolated areas and no great continuous expanses of uniformity as are found in the arctic area.

2. The frozen subsoil common to the north is lacking, as is also the mat of undecayed or partly decayed vegetation with a thickness of four or five inches to several feet, on which the climax forms.

3. Great masses of foliose lichens that form the climax dominants in the northern tundra (Shelford and Twomey, 1941) are absent and the climax assumes a different life form as sedges and grasses.

4. None of the larger influent mammals of the northern tundra is present in the alpine meadow. No mammal of any kind is confined to the alpine or particularly characteristic of it although a few species appear to reach their maximum abundance there. The pika is the most nearly characteristically alpine of any of the mammals, but it is confined to certain seral stages and can scarcely be considered a permanent.

5. On Mt. Timpanogos there are only two species of birds confined to the alpine area, and these mainly during the summer. Of these two the leucosticte is strictly mountainous, while the pipit is only subspecifically different from the tundra form. In most other portions of the western mountains the ptarmigan may be added to this list of birds. The great variety of breeding shorebirds and other types of birds common to the north is absent.

6. The invertebrates, particularly the insects, as far as they are at present known, show a peculiar mixture of northern, montane and lowland species, but the general aspect of insect life appears to more nearly resemble the plains grasslands. Such widely distributed species as *Lygus pratensis*, *Geocoris bullatus*, *Nysius californicus*, *Nysius ericae*, and *Agenotettix deorum* are common there. Grasshoppers, Hemiptera, and Homoptera play a conspicuous role in total populations as they do in the grasslands. Ants, although less abundant than in the low grasslands, are nevertheless present. There is no preponderance of Diptera as there is in the north. Some insects that are chiefly northern in distribution are: *Harpalas carbonatus*, *Coccinella transversoguttata*, *Hippodamia convergens*, *Adoxus obscurus*, *Arphia frigida*, *Formica fusca gilida* and *Vespula norvegica norvegicoides*.

7. Plants in general show a closer affinity to the northern species than do the animals. An analysis of Cox's (1933) list of plants from the alpine of James Peak, Colorado shows that about a third of the species are also transcontinentally distributed across the arctic. A list of 99 representative species from the alpine of Mt. Timpanogos shows that about 25% are arctic and transcontinental in distribution. A number also occur in the Old World. A list of northern species on Timpanogos includes the following: *Cryptogramma acrostichoides*,

*Felix fragilis*, *Lycopodium selago*, \**Phleum alpinum*, *Deschampsia caespitosa*, \**Trisetum spicatum*, \**Poa alpina*, *Carex eleocharis*, *Betula glandulosa*, *Polygonum bistortoides*, *Polygonum douglasii*, *Silene acaulis*, *Stellaria longipes*, *Cerastium beerlingianum*, *Sagina saginoides*, *Draba nivalis*, *Dasiophora fruticosa*, *Sibbaldia procumbens*, *Androsace subumbellata*, *Pedicularis groenlandica*, and *Erigeron compositus*. Only three of these (\*) are important in the climax on the mountains and none of them occur in tundra climax near Churchill, Manitoba.

8. Absence of the thick mats of foliose lichens in the alpine has already been mentioned. From lists of alpine plants available for the Rocky Mountains of Utah and Colorado, the heaths (Ericaceae) are not a conspicuous part of the alpine flora as they are in the northern tundra.

It would appear on analysis of the data at hand that any resemblance which the alpine holds with the northern tundra is due to the total climatic similarities of the two communities; while the differences between the two may be associated with the diversification in topography. At least two important topographic differences between the alpine and northern tundra are evident: First, the island-like nature, ruggedness, and relatively small area of alpine as compared to the vast and unbroken expanse of the tundra; and second, the close proximity of the alpine to more temperate communities of valleys, in contrast to the wide distances separating the arctic from temperate communities on more level terrain. This latter factor lends itself more readily to the migration into the alpine of those lowland species that are able to tolerate the climatic conditions extant.

The biota of the alpine communities, therefore, consists in the main of those lowland and montane forest species that are able to tolerate the essentially arctic climatic conditions found there or occur there only temporarily or during favorable seasons, and those typically northern species that are able to endure the combination of topographic characteristics common to the mountains. The factor of isolation which is fundamentally topographic in mountains plays an important role in these communities.

Limited area and isolation alone are sufficient to preclude the occurrence of the large herds of caribou that roam over the northern tundra and with them the group of large carivores that depends upon them for food. Migration habits long established and want of sufficient territory may well combine to exclude the shore birds and other avifauna common to the north.

It would seem that insofar as the alpine community is concerned,

the topographic features present are equally as important as the climatic characters in shaping the communities that exist. To the extent that these communities represent assemblages of organisms existing under a peculiar combination of climatic and topographic conditions, they surely constitute a singular set of communities distinct from all others. To this end the alpine might be considered as a community of biome rank even though it does not measure up to all the conditions commonly thought be requisite to that category.

Further investigations into the bio-ecology of the alpine communities of other portions of the West will surely be necessary before a final evaluation of the communities can be made.

### VIII. SUMMARY

1. This study includes an analysis of the major biotic communities of Mt. Timpanogos near Provo in the southern Wasatch Range of Utah and higher elevations of the western Uinta Mountains. Organisms were studied as far as possible from the standpoint of their distribution, populations, aspections and interactions.

2. Observations extended over a period of about 11 years from 1930 to 1941, with the most intensive period of work from 1937 to 1941. The greater part of the studies were made during the summer months. Methods employed included general observations on habits, distribution, etc., and quantitative sampling. Relative numbers of mammals above chipmunk size were estimated by cruising, counting dens, burrows, and other signs, and by counting fecal pellets. Smaller mammal populations were determined by the use of measured plots of one half acre (0.2 hectare) in which were set about 100 snap traps for four or five consecutive days. No effort was made to calculate influx or efflux so that the data are chiefly of comparative value. Bird populations were made available by cruising over 5 acre (2 hectare) areas in early morning or by watching smaller areas when cruising was not possible. Quantitative invertebrate samples were taken in all layer communities represented. One tenth square meter samples of the upper 2 inches of soil and leaf litter were taken and the invertebrates counted. In the vegetative layers, 48-50 sweeps with a net 30 centimeters in diameter were taken to represent one square meter. Series of specimens of all groups were preserved for identification purposes. Daily weather records were kept while field work was being done.

3. The general plan of treatment of the subject is to consider the



vegetation and the invertebrate animals as a biotic matrix; then the larger animals are treated from the viewpoint of their relationship to this matrix, especially as their life habits are associated with the various layer communities represented. Coactions and reactions of the larger species are brought into the discussion as far as they are understood.

4. Topography and geology of the regions are considered particularly with regard to the bearing they have on the biota. Mt. Timpanogos is shown to be an extremely rugged mountain in upper elevations with the result that the Upper Montane forests are able to develop only in scattered subclimax form. This condition is shown to have a great effect on the populations of animals and upon the presence or absence of certain constituents. On the other hand, relatively smooth contours and stable conditions in the high plateau of the Uinta Mountains have allowed the development of extensive Upper Montane climax forests with lower animal populations in general and with a number of true climax animals present.

5. The Montane Coniferous Forests and their seral stages are considered to be a portion of the Transcontinental Coniferous Forest Biome on the basis of a large number of organisms that are common to both and either specifically identical or ecologically equivalent. Presence of these organisms indicates a general similarity in living conditions that binds the northern and montane communities together.

6. Montane and Subalpine forests of Clements, recognized by him as distinct plant formations, are here reduced to associations as a result of including animals in the study. The term "Montane Forest" is used to indicate their close relationship, and they are designated as Lower and Upper Montane largely on the basis of their dominant plants, a few birds, and certain climatic differences. The close biotic relationship between these two communities is indicated by the fact that all the mammals, with the possible exception of one rare mouse, range through both forest types. There is a tendency for some species to be more abundant in one than in the other but in the case of the larger animals the numbers appear to be about the same. Of about 57 species of birds whose breeding range have been fairly accurately determined, about 61% are known to occur in both Upper and Lower Montane Forests. About 14% are confined to the Lower Montane and 10% to the Upper Montane. The remainder are found in valleys but range through both mountain types. There are also a large number of invertebrates found throughout both Montane Forests.

7. In the Lower Montane, the white fir-Douglas fir climax and

the aspen subclimax were studied in more or less detail. The former occurs as relatively small patches on north-facing slopes rather than as a continuous forest. It possesses a luxuriant shrubby and herbaceous growth in some places, but where the tree canopy is dense there is little vegetation on the forest floor. Low shrub-herb, tall shrub, and tree layers were recognized in the vegetation of this community. The aspen subclimax makes up the greater part of the Lower Montane forest on Mt. Timpanogos. There is a general tendency for the aspens to eventually be replaced by conifers, but in many places this is an extremely slow process due, in part at least, to the coactions of the deer, porcupine, and snowshoe rabbit which either kill the trees outright or retard their growth by eating off the terminal shoots. Herb, shrub, and tree layers were recognized in the vegetation of this community.

8. A comparison of the invertebrate population of the aspen subclimax and the conifer climax of the Lower Montane shows that the total numbers are greater in the aspens in all layer communities. The total invertebrate populations on trees are about four times greater in the aspens. In the ground layer ants are very important in both communities, living under logs and rocks as well as in open areas. Many of the species also climb up into the vegetational layers. Beetles and spiders are also an important feature of the ground layer. Leafhoppers are the most abundant invertebrates in the herb and shrub layers of both communities. In the tree layer there is a striking difference in the invertebrate constituents. In the aspens, leafhoppers of about 4 species comprise about 87% of the total invertebrate population, while in the conifers they form only about 4%. On the other hand, spiders and Diptera are more abundant in the conifers. Spiders make up about 37% of the population in the conifers and less than 1% in the aspens. Diptera form about 50% of the population in conifers and only about 1% in the aspens.

9. All of the larger mammals and birds and many of the smaller ones range through both aspens and conifers. A certain group of hole-nesting birds including several species of woodpeckers, swallows, martins, and house wrens are confined mainly or entirely to aspens; while nuthatches and kinglets are mostly in conifers. The red squirrel (*Tamiasciurus*) is strictly confined to the conifers. Gophers and ground squirrels are much more abundant in the aspen forests and seldom enter the climax communities if they are very extensive. Bird populations are higher in the aspens at all seasons except winter.

10. Studies of the Upper Montane Forests were carried out in

the climax type as it is found in the Uinta Mountains and in the subclimax as found on Mt. Timpanogos. The climax forests consist of dense and extensive stands of Engelmann spruce and alpine fir. The undergrowth is made up of low shrubs and herbs of about the same height and mixed intimately together. There is no tall shrub layer as in the Lower Montane. The Upper Montane forests of Mt. Timpanogos are in the form of a subclimax of scattered Engelmann spruce and alpine fir interspersed with a dense growth of shrubs and herbs. Herb, shrub, and tree layers may be recognized. Continuous climax forests are unable to develop here because of a number of active physical forces including rapid erosion, steepness of slopes, and snowslide action.

11. Invertebrate population studies in these two communities of the Upper Montane, revealed that in most layers the numbers were far greater in the subclimax. Ground populations showed a lower figure in both communities. Ants were less abundant than in the Lower Montane. In the herb layer there were about nine times more invertebrates in the subclimax. This is due to the presence of large numbers of leafhoppers of the genus *Dikraneura* as well as considerable numbers of Hemiptera in the subclimax. The population in trees was about six times greater in the subclimax. Leafhoppers were again an important factor. Spiders were more abundant in the climax, but even there were less numerous than in the Lower Montane climax. Diptera were comparatively more abundant in the climax forests where they made up about 40% of the invertebrate population on herbs and 60% on trees.

12. All of the large vertebrates such as the deer and larger carnivores range also into the Upper Montane climax and subclimax as well as many of the earlier seral stages. One mammal, *Phenacomys intermedius*, seems to be confined to the Upper Montane subclimax but it is so rare that this has not been definitely established. About 5 species of birds, including the Rocky Mountain pine grosbeak, Rocky Mountain jay, and alpine three-toed woodpecker, seem to be confined to the Upper Montane during the breeding season and most of them stay there throughout the year. Marmots and pikas reach their greatest abundance in early xeroseral stages in the Upper Montane but extend down into the Lower Montane as well. The common *Peromyscus maniculatus* is less abundant at higher elevations particularly in early summer. Taking populations of small mammals as a whole, plot trapping indicated that the population in the subclimax Upper Montane was about 2.5 times greater than in the climax. This was partly

due to late summer increase in the subclimax, possibly resulting from some influx of animals from lower elevations. Bird populations throughout the summer were about five times greater in the subclimax than in the climax forests of the Uintas. This high population of vertebrates in the open subclimax type of community characteristic of the upper elevations of Mt. Timpanogos, corresponds with a greater amount and variety of both invertebrate and plant foods, and suggests that foods may be the governing factor.

13. Certain mammals and birds appear to be strictly or almost entirely confined to the climax. The martin is quite rare at the present time but indications are that it is confined to the climax and does not occur in the subclimax of Mt. Timpanogos. The red squirrel seems to require a continuous conifer forest at least an acre in extent. It is rarely found in the Upper Montane of Mt. Timpanogos. The Rocky Mountain jay, alpine three-toed woodpecker, and pine grosbeak are absent from Mt. Timpanogos in summer, yet they are common species in the climax of the Uintas.

14. The mule deer, porcupine and snowshoe rabbit are the larger vertebrates now present in greatest numbers in the Montane Forest. In the aspen subclimax they may be considered as dominants since they effectively control the replacement of the aspens by conifers as already mentioned. In the Lower Montane climax the porcupine is gradually removing the white fir from the community by killing most of the young trees and girdling the larger ones near the top. Nearly all of the predatory mammals are exterminated or so nearly so that they play little part in the community. The only ones of consequence are the badger and coyote which still persist in considerable numbers and feed largely on ground squirrels and pocket gophers during the summer.

15. General observations were made on the seral development of the communities, but no quantitative data are available for the earlier stages. In general it may be said that the development of communities in mountains is an extremely slow process due to the great activity of physical forces and the short periods of growth and activity. In stabilizing communities organisms have great obstacles to overcome in the way of physical and biotic retroactive forces and comparatively little time to do it in.

16. The alpine meadow, in which grasses and sedges are dominant, appears to represent the climax community and occurs in relatively level basins where some soil has been able to accumulate.

17. The biotic matrix, of the alpine meadow is divided into ground



and herb layer societies. Invertebrate populations of the ground layer are low and consist mainly of mites, beetles, burrowing Hemiptera, and ants. The most abundant invertebrates on herbs are leafhoppers and various Hemiptera.

18. No species of mammal is confined to the alpine although the pika and marmot reach their greatest abundance there in early xeroseral stages. A number of animals common to lower elevations also occur in the alpine. These include the pocket gopher, two species of ground squirrels, mule deer, weasel, badger and coyote. The white-footed mouse is the only cricetid found thus far in the alpine and it seems to occur there only in the summer and autumn.

19. Breeding birds are very few in the alpine of Mt. Timpanogos. The mountain pipit, black leucosticte and rock wren are the most common. This area is also visited by most of the large predatory birds.

20. Succession was studied only superficially, but there appear to be at least two hydroseres and three xeroseres.

21. The alpine resembles the tundra communities with respect to certain climatic conditions. Some animals and about 25% of the plants are identical with transcontinental arctic species. However, few or none of them are important in the arctic climax. It differs from the arctic in having a different life form (sedges and grasses rather than foliose lichens) as the dominant vegetation. It also lacks the large permeant influents and most of the characteristic animals peculiar to the northern tundra.

22. Alpine communities, as found on Mt. Timpanogos and other more southern mountainous areas, seem to consist of those northern species that can tolerate the combination of topographical features common to high mountains, and those lowland species that are able to endure the essentially arctic climate of the high altitudes. To this end the alpine comprises a peculiar set of communities which may be considered most nearly in the category of a biome, even though it is lacking in some of the features generally considered to be concomitant to that term.

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## APPENDIX A

Distributional list of the mammals and birds of the Montane Forests of Mt. Timpanogos and western Uintas. Most of the records are based on collections. No hypothetical species are included.

C—Climax or subclimax only. S—Seral stages only.

Sc—Both seral and climax stages.

	Lower Montane Climax	Aspen Subclimax	Upper Montane Climax	Upper Montane Subclimax
<i>Sorex vagrans monticola</i> (Merriam)	Sc	Sc	Sc	Sc
Arizona Mountain Shrew				
<i>Sorex (Neosorex) palustris navigator</i> (Baird)	S	S	S	S
Rocky Mt. Water Shrew				
<i>Myotis volans interior</i> Miller	Sc	Sc	Sc	Sc
Interior Long-legged Bat				
<i>Nycteris cinerea</i> (Beauvois)	Sc	Sc	Sc	Sc
Hoary Bat				
<i>Corynorhinus rafinesquii pallescens</i> Miller	Sc	Sc	Sc	Sc
Pallid Lump-nosed Bat				

<i>Euarctos americanus</i> ssp. Black Bear	Sc	Sc	Sc	Sc
<i>Martes caurina origenes</i> (Rhoads) Rocky Mountain Marten	C?		C	
<i>Mustela frenata nevadensis</i> Hall Nevada Weasel	Sc	Sc	Sc	Sc
<i>Mustela vison energumenos</i> (Bangs) Western Mink	S	S	S	S
<i>Mephitis occidentalis major</i> (Howell) Great Basin Striped Skunk	Sc	Sc	?	?
<i>Taxidea taxus</i> ssp. Badger	Sc	Sc	S	Sc
<i>Canis latrans lestes</i> Merriam Great Basin Coyote	Sc	Sc	Sc	Sc
<i>Felis oregonensis hippolestes</i> (Merriam) Rocky Mountain Cougar	Sc	Sc	Sc	Sc
<i>Lynx uinta</i> Merriam Mountain Bobcat	Sc	Sc	Sc	Sc
<i>Marmota flaviventris nosophora</i> Howell Golden Mantled Marmot	S	S	S	Sc
<i>Citellus variegatus utah</i> Merriam Utah Rock Squirrel	S			
<i>Citellus armatus</i> (Kennicott) Uinta Ground Squirrel	Sc	Sc	Sc	Sc
<i>Citellus lateralis castanurus</i> (Merriam) Wasatch Mantled Ground Squirrel	S	S	S	S
<i>Eutamias quadrivittatus umbrinus</i> (Allen) Uinta Chipmunk	Sc		Sc	Sc
<i>Eutamias minimus consobrinus</i> (Allen) Wasatch Chipmunk	Sc	Sc	Sc	Sc
<i>Tamiasciurus hudsonicus ventorum</i> (Allen) Wind River Mt. Red Squirrel	C			C
<i>Tamiasciurus fremonti fremonti</i> Aud. & Bach. Fremont Red Squirrel			C	
<i>Glaucomys sabrinus lucifugus</i> Hall Utah Flying Squirrel	Sc	?	Sc	Sc
<i>Thomomys talpoides moorei</i> Goldman Moore Pocket Gopher	S	Sc	S	Sc
<i>Castor canadensis</i> ssp. Beaver	S	S	S	
<i>Peromyscus maniculatus</i> ssp. White-footed Mouse	Sc	Sc	Sc	Sc
<i>Neotoma cinerea acraia</i> (Elliott) Bushy-tailed Wood Rat	Sc	Sc	?	?
<i>Phenacomys intermedius intermedius</i> Merriam Gale Red-backed Mouse			Sc	Sc
<i>Microtus montanus nanus</i> (Merriam) Dwarf Meadow Mouse	S	S	S	S
<i>Microtus mordax mordax</i> (Merriam)	Sc	Sc	Sc	Sc



Cantankerous Meadow Mouse				
<i>Microtus richardsoni macropus</i> (Merriam)	S	S	S	S
Big-footed Meadow Mouse				
<i>Ondatra zibethica osoyoosensis</i> (Lord)	S	S	S	
Rocky Mountain Muskrat				
<i>Zapus princeps utahensis</i> Hall	S	Sc	?	Sc
Utah Jumping Mouse				
<i>Erethizon epixanthum epixanthum</i> Brandt	Sc	Sc	Sc	Sc
Yellow-haired Porcupine				
<i>Ochotona princeps uinta</i> (Hollister)	S	S	S	S
Uinta Pika				
<i>Lepus bairdi bairdi</i> Hayden	C	C	C	C
Rocky Mt. Snowshoe Rabbit				
<i>Cervus canadensis canadensis</i> (Erxleben)	Sc	Sc		Sc
American Wapiti				
<i>Odocoileus hemionus macrotis</i> (True)	Sc	Sc	Sc	Sc
Mule Deer				
<i>Ardea herodias treganzai</i> Court	S	S	S	
Treganza's Heron				
<i>Leucophorix thula brewsteri</i> (Thayer & Bangs)	S			
Brewster's Egret				
<i>Nycticorax nycticorax hoactli</i> (Gmelin)	S			
Black-crowned Night Heron				
<i>Anas platyrhynchos platyrhynchos</i> L.	S	S	S	
Common Mallard				
<i>Bucephala clangula americanus</i> (Bonap.)	S	S		
American Golden-eye				
<i>Bucephala albeola</i> (Linnaeus)	S	S		
Buffle-head				
<i>Anas acuta tztzihoa</i> (Vieillot)			S	
Pintail				
<i>Mergus serrator</i> Linnaeus	S	S		
Red-breasted Merganser				
<i>Cathartes aura teter</i> Fried.	Sc	Sc		
Turkey Vulture				
<i>Accipiter gentilis atricapillus</i> (Wilson)	C	C	C	C
Eastern Goshawk				
<i>Accipiter striatus velox</i> (Wilson)	C	C	C	C
Sharp-shinned Hawk				
<i>Accipiter cooperi</i> (Bonaparte)	C	C	C	C
Cooper's Hawk				
<i>Buteo jamaicensis calurus</i> Cassin	Sc	Sc	Sc	Sc
Western Red-tail				
<i>Aquila chrysaëtos canadensis</i> (L.)	Sc	Sc	Sc	Sc
Golden Eagle				
<i>Pandion haliaëtus carolinensis</i> (Gmelin)			Sc	
Osprey				
<i>Falco mexicanus</i> Schlegel	S	S	S	S
Prairie Falcon				

<i>Falco sparverius sparverius</i> L.	Sc	Sc		
Eastern Sparrow Hawk				
<i>Dedragapus obscurus obscurus</i> (Say)	Sc	Sc	Sc	Sc
Dusky Grouse				
<i>Bonasa umbellus incanus</i> Aldr. & Fried.	Sc	Sc		
Ruffed Grouse				
<i>Actitis macularia</i> (L.)	S	S	S	
Spotted Sandpiper				
<i>Zenaidura macroura marginella</i> (Woodh.)	Sc	Sc		
Western Mourning Dove				
<i>Otus flammeolus</i> (Kaup)	C?	C		
Flammulated Screech Owl				
<i>Bubo virginianus occidentalis</i> Stone	Sc	Sc	Sc	Sc
Montana Horned Owl				
<i>Glaucidium gnoma pinicola</i> Nelson	C		?	?
Rocky Mountain Pvgmy Owl				
<i>Aëronautes saxatalis saxatalis</i> (Wood.)	S	S	S	S
White-throated Swift				
<i>Selasphorus platycercus platycercus</i> (Swain)	Sc	Sc	Sc	Sc
Broad-tailed Hummer				
<i>Selasphorus rufus</i> (Gmelin)	Sc	Sc	Sc	Sc
Rufous Hummer (Visitant only)				
<i>Stellula calliope</i> (Gould)	Sc	Sc	?	?
Calliope Hummingbird				
<i>Sphyrapicus varius nuchalis</i> Baird	C	C	C	
Red-naped Sapsucker				
<i>Sphyrapicus thyroideus nataliae</i> (Malherbe)	C	C	C	
Natalie's Sapsucker				
<i>Colaptes cafer collaris</i> Vigors	Sc	Sc	Sc	Sc
Red-shafted flicker				
<i>Dryobates villosus monticola</i> Anthony	C	C	C	C
Rocky Mt. Hairy Woodpecker				
<i>Dryobates pubescens leucurus</i> (Hart.)		C		
Batchelder's Woodpecker				
<i>Picoides tridactylus dorsalis</i> Baird			C	
Alpine Three-toed Woodpecker				
<i>Empidonax hammondi</i> (Xantus)	C	C		
Hammond's Flycatcher				
<i>Empidonax difficilis difficilis</i> Baird	Sc	Sc	Sc	Sc
Western Flycatcher				
<i>Myiochanes richardsonii richardsonii</i> (Swains)	Sc	Sc		Sc
West. Wood Pewee				
<i>Nuttallornis borealis borealis</i> (Swainson)			Sc	
Olive-sided Flycatcher				
<i>Tachycineta thalassina lepida</i> Mearns		C		
Violet Green Swallow				
<i>Iridoprocne bicolor</i> (Vieillot)		C	C?	
Tree Swallow				
<i>Petrochelidon albifrons hypopolia</i> Oberholser	S	S	S	S

Cliff Swallow				
<i>Progne subis subis</i> (Linnaeus)	C			
Purple Martin				
<i>Perisoreus canadensis capitalis</i> Ridgway			Sc	
Rocky Mt. Jay				
<i>Cyanocitta stelleri</i> ssp.	Sc	Sc		
Crested Jay				
<i>Nucifraga columbiana</i> (Wilson)			Sc	Sc
Clark's Nutcracker				
<i>Parus atricapillus nevadensis</i> (Linsdale)	C	C		
Nevada Black-capped Chickadee				
<i>Parus gambeli gambeli</i> (Ridgway)	C	C	C	C
Mountain Chickadee				
<i>Sitta carolinensis nelsoni</i> Mearns	C	C	C	IC
Rocky Mountain Nuthatch				
<i>Sitta canadensis</i> Linnaeus	C			
Red-breasted Nuthatch				
<i>Certhia familiaris montana</i> Ridgway	C		C	C
Rocky Mountain Creeper				
<i>Cinclus mexicanus unicolor</i> Bonap.	S	S	S	S
Dipper				
<i>Troglodytes aedon parkmanii</i> Audubon	C	C		
Western House Wren				
<i>Salpinctes obsoletus obsoletus</i> (Say)	S	S	S	S
Rock Wren				
<i>Turdus migratorius propinquus</i> Ridgway	Sc	Sc	Sc	Sc
Western Robin				
<i>Hylocichla guttata auduboni</i> (Baird)	Sc	Sc	Sc	Sc
Audubon's Hermit Thrush				
<i>Hylocichla ustulata almae</i> Oberholser	S	S	?	?
Olive-backed Thrush				
<i>Sialia currucoides</i> (Bechstein)	Sc	Sc	Sc	Sc
Mountain Bluebird				
<i>Myadestes townsendi</i> (Audubon)			Sc	Sc
Townsend's Solitaire				
<i>Regulus regulus olivaceus</i> Baird	C		C	C
Western Golden-crowned Kinglet				
<i>Regulus calendula cinereus</i> (Grinnell)	C		C	C
Western Ruby-crowned Kinglet				
<i>Anthus rubescens alticola</i> Todd			S	S
Rocky Mountain Pipit				
<i>Vireo gilvus leucopolius</i> Oberholser		C		
Oregon Warbling Vireo				
<i>Vermivora celata orestera</i> (Say)	C	C	C	C
Mountain Orange-crowned Warbler				
<i>Dendroica auduboni memorabilis</i> Ober.	C	C	C	C
Mountain Audubon Warbler				
<i>Piranga ludoviciana</i> (Wilson)	C	C		
Western Tanager				

<i>Hedymeles m. melanocephalus</i> (Swainson)	Sc	Sc		
Rocky Mountain Black-headed Grosbeak				
<i>Passerina amoena</i> (Say)	Sc	Sc		
Lazuli Bunting				
<i>Carpodacus cassinii</i> Baird	Sc	Sc	Sc	Sc
Cassin's Purple Finch				
<i>Pinicola enucleator montana</i> Ridgway			C	
Rocky Mountain Pine Grosbeak				
<i>Hesperiphona vespertina brooksi</i> Grinnell	C	C?	?	?
Western Evening Grosbeak				
<i>Spinus pinus pinus</i> (Wilson)	C	C	C	C
Northern Pine Siskin				
<i>Loxia curvirostra bentii</i> Griscom	C		C	
Bent's Crossbill				
<i>Junco caniceps</i> (Woodhouse)	Sc	Sc	Sc	Sc
Gray-headed Junco				
<i>Zonotrichia leucophrys oriantha</i> Ober.			Sc	Sc
White-crowned Sparrow				
<i>Passerella iliaca schistacea</i> Baird	S	S	S	S
Slate-colored Fox Sparrow				
<i>Melospiza lincolni alticola</i> Miller & McCabe	S	S	S	S
Lincoln Sparrow				
<i>Spizella passerina arizonae</i> Coues	C	C	C	C
Western Chipping Sparrow				

## APPENDIX B

List of invertebrates taken in samples from the climax and sub-climax communities and identified at least as far as genus. This list does not imply that the species are necessarily limited in distribution to the particular places in which they were taken, although many of them undoubtedly are. The key to abbreviations used in the list is as follows: G—ground layer, H—herb layer, S—shrub layer, T—tree layer, LMC, Lower Montane climax, AS—Aspen subclimax, UMC—Upper Montane climax, UMS—Upper Montane subclimax.

## Mollusca

## Helicidae

- Microphysula ingersolli* (Bland).....G: LMC, UMS  
*Oreohelix strigosa depressa* (Cock.).....G: LMC, AS, UMS

## Zonitidae

- Vitrina alaskana* Dall.....G: LMC, AS, UMS  
*Euconulus fulvus alaskensis* (Pils.)..G: LMC, AS, UMC, UMS  
*Zonitoides arborea* (Say).....LMC, AS

## Valloniidae

- Vallonia albula* Sterki.....G: LMC, AS



## Pupillidae

*Vertigo modesta corpulenta* (Morse).....G: LMC, AS

## Chilopoda

## Henicopidae

*Zygethobius dolichopus* (Chamberlin).....G: UMC

## Lithobiidae

*Pokabius utahensis* (Chamberlin).....G: AS, UMC

*Bothropolys permudus* (Chamberlin).....G: LMC, AS

## Chilenophilidae

*Gnathomerium xenoporus* (Chamberlin).....G: LMC, AS

## Diplopoda

*Taiulus tiganus* (Chamberlin).....G: LMC, AS

*Nemasoma uta* Chamberlin.....G: LMC, AS

*Oriulus medianus* (Chamberlin).....G: LMC, AS

## Araneida

## Gnaphosidae

*Zelotes subterraneus* Koch.....G: LMC, AS, UMS

*Gnaphosa gigantea* Keys.....G: UMS

## Agelenidae

*Cicurina garrina* Chamberlin.....G: LMC

## Clubionidae

*Clubiona* sp.....H: LMC; S: LMC, AS

## Attidae

*Metaphidippus nigromaculatus* Keys.

H: UMS; S: UMS; T: UMS

*Paraphidippus marginatus*.....S: LMC

## Argiopidae

*Aranea displicata* Htz.....H: LMC; T: LMC, UMS

*Aranea* sp.....T: LMC, UMC

*Metopeira foxi* G. and I.....G: AS; T: UMS

*Tetragnatha* sp.....T: LMC

## Dictynidae

*Dictyna stulta* Gertsch.....T: LMC

*Dictyna uintana* Chamberlin.....H: LMC; S: LMC, AS

*Dictyna completa* Chamberlin.....T: UMC

## Lycosidae

*Pardosa mackenziana* Keys.....G: AS, UMC

*Lycosa orophila* Chamb. and Gertsch.....G: AS

*Lycosa* sp.....G: AS

## Theridiidae

*Theridium placens* Keys.....S: LMC; T: LMC

*Theridion* sp.....H: LMC

## Thomisidae

*Philodromus pacificus* Banks.....T: LMC

## Linyphiidae

*Ceraticelus crassiceps* Chamb. and Ivie.....H: UMS

*Lepthyphantes nebulosus* Sund.....G: UMS

## Orthoptera

## Locustidae

- Camnula pellucida* Scudder.....H: AS  
*Circotettix verruculatus* (Kirby).....H: AS  
*Melanoplus marshallii marshallii* Thom.....H: UMC

## Neuroptera

## Chrysopidae

- Chrysopa californica* Cog.....H and S: LMC, AS, UMC, UMS

## Homoptera

## Aphidae

- Macrosiphum* (near) *albifrons* Essig.....H: UMS  
*Macrosiphum rudbeckiae* (Fitch).....S: AS  
*Macrosiphum stanleyi* (Wilson).....S: AS  
*Macrosiphum atripes* G.-P.....H: LMC  
*Macrosiphum solanifolii* (Ashm.).....H: AS  
*Macrosiphum valerinae* (Clarke).....H: AS  
*Macrosiphum timpanogos* K.....H: UMS  
*Mindarus abietinus* Koch.....H: LMC  
*Myzus haywardi* Knowlton.....H: AS  
*Myzus monardae* Williams ?.....S: LMC  
*Amphorophora* (near) *rubi* (Kalt.).....H: LMC  
*Chaitophorus populifoliae* Oestlund.....T: AS  
*Myzocallis alhambra* Davidson.....S: AS  
*Cinara lasiocarpae* G.-P.....T: UMC  
*Cinara osborni* Knowlton.....T: LMC

## Cicadellidae

- Idiocerus suturalis* Fitch.....H: AS; S: AS; T: AS  
*Idiocerus lachrymalis* Fitch.....S: AS; T: AS  
*Idiocerus formosus* Ball.....H: AS; S: AS; T: AS  
*Thamnotettix cockerelli* Ball.....H: UMS; S: UMS  
*Thamnotettix citrinifrons* G. & B.....H: UMS; T: UMS  
*Thamnotettix flavocapitatus* Van D.....H: UMS; T: UMS  
*Thamnotettix geminatus* Van D.....H: AS, UMS; S: AS, UMS  
*Thamnotettix belli* (Uhl.).....H: AS  
*Macrosteles divisa* (Uhl.).....S: UMC  
*Macrosteles variata* (Fall).....H: AS, UMS  
*Deltocephalus grex* Oman.....H: AS, UMS; S: UMS  
*Deltocephalus dorsti* Oman.....H: UMC, UMS  
*Laevicephalus debilis* (Uhl.).....T: UMS  
*Latalus misellus* (Ball).....H: LMC  
*Dikraneura carneola* (Stal.)

H: LMC, AS, UMC, UMS; S: AS; T: LMC, UMC, UMS

- Empoasca* sp. (fabae group).....H: LMC, AS  
*Empoasca pectinata* Del.....S: AS  
*Nesosteles neglectus* (Del. & D.).....H: AS  
*Balclutha punctata* (Thunb.).....H: AS, UMS  
*Erythroneura aspera* B. & C.....H: LMC; S: LMC  
*Parabolocratus viridis* (Uhl.).....H: LMC

## Membracidae

- Stictocephala gillettei* Godg.....H: LMC  
*Ceresa basalis turbida* Godg.....H: UMS

## Psyllidae

- Trioza* sp.....T: UMC; S: UMS  
*Trioza maura* Forst.....S: UMS  
*Psylla americana* Crawf.....T: UMC, UMS  
*Psylla brevistigmata acuta* Crawf.....S: UMC  
*Arytaina ribesiae* (Crawf.).....T: UMS  
*Aphalara samila* Caldwl.....H: AS; T: UMC, UMS

## Hemiptera

## Pentatomidae

- Chlorochroa congrua* Uhler.....S: AS  
*Trichopepla atricornis* Stal.....H: UMS  
*Banasa dimidiata* (Say).....S: AS

## Miridae

- Lygus pratensis* (Linn.).....H: LMC, UMS; S: UMS  
*Dicyphus discrepens* Knight.....H: AS  
*Dicyphus agilis* (Uhler).....S: UMS  
*Coquillettia insignis* Uhler.....H: UMS  
*Polymerus tumidifrons* Knight.....H: UMS  
*Deraeocoris nebulosus* Uhler.....S: LMC  
*Deraeocoris Bakeri* Knight.....T: UMS  
*Phytocoris intepersus* Uhler.....S: LMC  
*Plagiognathus obscurus* Uhler.....S: AS

## Nabidae

- Nabis alternatus* Parsh.H: LMC, AS, UMS; S: LMC, AS, UMS

## Lygaeidae

- Scolopostethus thomsoni* Reuter.....G: AS  
*Nysius californicus* Stal.....H: UMS  
*Nysius ericae* (Schilling).....H: AS  
*Lygaeus kalmii* Stal.....T: UMS

## Anthocoridae

- Anthocoris antevolens* White.....T: AS  
*Anthocoris melanocerus* Reuter.....H: AS, UMS; S: AS  
*Tetraphleps furvus* Van Duzee.....T: UMC

## Coleoptera

## Carabidae

- Harpalus rufimanus* Lec.....G: AS  
*Calathus reductus* Csy.....G: AS  
*Amara hesperia* Csy.....G: AS  
*Metabletus americanus* (Dej.).....G: AS  
*Pterostichus protractus* Lec.....G: LMC, AS, UMS  
*Nebria obtusa* Lec.....G: UMC, UMS  
*Pterostichus angusticollis* Csy.....G: AS, UMC  
*Calosoma frigidum* Kby.....G: AS  
*Nebria sahlbergi* Fisch.....G: UMC  
*Callisthenes striatulus* (Lec.).....G: AS

- Staphylinidae  
*Tachyporus rulomus* Blkwr.....G: AS  
*Quedius laevigatus* (Gyll.).....G: UMC
- Coccinellidae  
*Adalia annectans* Cr.....T: LMC  
*Coccinella transversoguttata* Fald.....T: UMC; H: UMS  
*Hippodamia convergens* Guer.....H: UMS  
*Psyllobora taedata* Lec.....H: LMC, AS  
*Cycloneda polita* Csy.....T: AS  
*Exochomus californicus* Csy.....G: UMC
- Tenebrionidae  
*Iphtimus serratus* (Mann.).....G: AS  
*Eleodes pimelioides* Mann.....G: AS
- Lucanidae  
*Platycerus marginalis* Csy.....G: AS
- Chrysomelidae  
*Orsodacne atra* (Ahr.).....S: AS  
*Phyllotreta* sp.....T: AS, UMS  
*Haltica tombacina* Mann. ?.....H: AS  
*Adoxus obscurus* (L.).....H: UMS  
*Syneta carinata* (Mann.).....T: UMS
- Buprestidae  
*Agrilus politus* (Say).....S: LMC
- Elateridae  
*Hypnoidus lucidulus* (Mann.).....C: UMS
- Cerambycidae  
*Callidium violaceum* (L.).....H: UMS  
*Spondylis upiformis* Mann.....H: UMS  
*Stenocorus vestitus* Hald.....T: LMC
- Scolytidae  
*Hylurgops porosus* (Lec.).....T: UMC
- Erotylidae  
*Dacne uteana* Csy.....H: UMS
- Ostomidae  
*Ostoma ferruginca* (L.).....H: UMS
- Melandryidae  
*Incolia longipennis* Csy.....S: AS; H: UMS; T: UMS
- Cantharidae  
*Silis munita* Lec.....H: LMC
- Mordellidae  
*Anaspis rufa* Say.....S: LMC, AS; T: UMC  
*Anaspis atrata* Champ.....S: UMS
- Melyridae  
*Hoppingiana hudsonica* Lec.....T: UMS
- Rhynchophora  
*Thricolepis inornata* Horn.....S: LMC  
*Dyslobus wasatchensis* Tanner.....H: LMC; S: LMC  
*Magdalis gentilis* Lec.....S: UMS  
*Hyperodes porcellus* (Say).....G: UMC



## Diptera

## Calliphoridae

*Protophormia terrae-novae* (R. D.).....T: UMS

## Empididae

*Rhamphomyia* sp.....S: LMC, AS; H: AS, UMS

*Platypalpus* sp.....H: UMC, UMS

## Rhagionidae

*Symphoromyia fulvipes* Bigot.....H: AS; S: LMC, AS

## Agromyzidae

*Agromyza affinis* Mall.....H: AS; S: AS

*Agromyza* sp.....T: UMC

*Phytomyza flavicornis* Fal.....H: AS

*Cerodontha dorsalis* Loew.....H: UMS; S: UMC; T: UMC

## Sepsidae

*Sepsis signifera* Mel.-Spul.....H: UMS; S: UMS

## Tachinidae

*Wagneria helymus* (Walker).....S: LMC

*Steveniopsis sinuata* Tns.....H: AS

*Leucostoma atra* Tns.....H: AS

## Trupaneidae

*Trupanea radifera* Coq.....H: UMS

*Tephritis clathrata* Lw.....H: UMS

## Tabanidae

*Chrysops noctifer* O. S.....S: LMC

## Chloropidae

*Oscinella frit* (Linn.).....H: UMS

*Meromyza saltatrix marginata* Becker.....H: LMC

*Chlorops stigmata* Becker.....T: UMS

## Sapromyzidae

*Sapromyza* .....H: AS

*Lauxania* sp.....T: AS

*Minnettia lupulina* (F.).....S: LMC; T: LMC

## Dolichopodidae

*Sympycnus* sp.....S: LMC

*Chrysotimus pusio* Loew.....H: LMC; S: LMC, AS

*Hercostomus unicolor* Loew.....S: LMC; H: AS; T: UMS

*Dolichopus blandus* V. D.....H: AS; S: AS

*Chrysotus* sp.....H: AS

*Campsicnemus nigripes* V. D.....S: UMC

## Sarcophagidae

*Sarcophaga peniculata* Pk.....S: AS

## Ephydriidae

*Philygria debilis* Loew.....S: AS; T: UMC

*Scatella sibilans* (Haliday).....H: UMC; T: UMC

*Scatella stenhammari* (Zetterstedt).....H: LMC

## Syrphidae

*Platycheirus angustatus* Zett.....H: AS

*Melanostoma* sp.....H: AS

*Metasyrphus luniger* Mg.....S: LMC; T: LMC

<i>Metasyrphus lapponicus</i> Zett.....	S: LMC; T: LMC
<i>Syrphus opinator</i> O. S.....	S: LMC; T: LMC
<i>Scatza pyrastris</i> L.....	S: LMC; T: LMC

## Anthomyiidae

*Schoenomyza dorsalis sulfuriceps* Mall.

H: UMS, UMC; T: UMS

*Schoenomyza* sp.....T: UMS*Fannia* sp.....H: LMC, AS; S: LMC*Hylemyia seamansi* Huck.....H: AS; S: AS*Hylemyia alcatheae* (Walker).....S: AS*Hylemyia* (near) *angusta* Stein.....H: AS*Lasiops spiniger* (Stein).....S: AS; T: AS*Spilogona* sp.....T: AS, UMC, UMS*Pegomyia* sp.....T: UMC*Hammomyia maculata* Stein.....S: UMS*Hoplogaster mollicula* Fallen.....S: LMC*Limosia anthracina* (Malloch).....S: LMC; T: LMC*Limosia nigrescens* (Stein).....S: UMC*Paregle cinerella* (Fallen).....T: UMC, UMS; H: UMS*Morellia micans* Mgt.....S: AS*Ileemyia* (near) *trivittata* (Stein).....T: UMS*Scatophaga grisea* Mall.....H: UMS

## Hymenoptera

## Formicidae

*Tapinoma sessile* (Say).....G: LMC; H: LMC*Formica neogagates lasioides* Emery

G: LMC; H: LMC; S: LMC

*Formica* sp. (rufa group).....G: AS; T: AS*Formica fusca gelida* Wheeler

G: LMC, AS, UMC, UMS; S: LMC, UMC, UMS; T: AS

*Formica sanguinea subnuda* Emery

G: LMC, AS; H: AS; T: AS

*Myrmica scabrinodis* Nylander..G: LMC, AS; H: LMC; S: AS*Camponotus sansabeanus vicinus* Mayr.....G: LMC; S: LMC*Camponotus herculeanus whymperi* Forel

G: LMC, AS, UMC, UMS; S: AS; T: LMC, AS

*Leptothorax acervorum canadensis* Prov.

G: LMC, AS, UMC, UMS; H: LMC, UMS;

S: LMC, AS, UMC, UMS

*Lasius niger neoniger* Emery

G: LMC, AS; H: AS; S: LMC; T: AS

## Vespididae

*Odynerus* sp.....T: UMS*Vespula pennsylvanica* Sauss.....G: AS; S: AS; T: AS*Vespula maculata* (Linn.).....H: AS*Vespula arenaria* (Fab.).....H: AS; T: AS; S: AS*Vespula norvegica norvegicoides* Sl.....H: AS*Vespula vulgaris* (Linn.).....G: AS

<i>Pseudomasaris edwardsi</i> (Cress.)	H: AS
Megachilidae	
<i>Osmia cyanella</i> Ckll.	S: AS
<i>Osmia</i> sp.	S: AS
<i>Megachile</i> sp.	S: AS
<i>Megachile inermis</i> (Prov.)	S: AS
Bremidae	
<i>Bremus appositus</i> Cress.	H: LMC, AS
<i>Bremus occidentalis</i> (Greene)	H: LMC, AS, UMS
<i>Bremus centralis</i> (Cress.)	H: LMC, AS
<i>Bremus bifarius</i> (Cress.)	H: AS, UMS
<i>Bremus rufocinctus</i> (Cress.)	H: LMC, AS
Hylaeidae	
<i>Hylaeus modestus</i> (Say)	S: UMS
<i>Hylaeus</i> sp.	H: UMS
Halictidae	
<i>Halictus</i> (Evyllaeus) sp.	H: UMS
<i>Halictus</i> (Chloralictus) sp.	H: AS
<i>Halictus rubicundus</i> (Christ.)	S: AS
Tenthredinoidea	
<i>Xyela</i> sp.	G: UMC
<i>Pleroneura aldrichi</i> Ross.	H: UMC
<i>Tenthredo</i> sp.	H: UMS
<i>Pachynematus</i> sp.	H: UMS
Braconidae	
<i>Meteorus reticulatus</i> Mues.	T: LMC
<i>Meteorus vulgaris</i> (Cress.)	H: AS; S: AS
<i>Microbracon xanthonotus</i> (Ashm.)	H: UMS
<i>Microbracon hyslopi</i> Vier.	H: UMS
<i>Opius</i> sp.	S: AS; T: AS
<i>Chelonus</i> (near) <i>proteus</i> Gahan.	H: AS
<i>Dacnusa</i> sp.	H: AS
<i>Aspilota</i> sp.	H: LMC
<i>Rogas</i> sp.	T: LMC; H: AS
<i>Aphidius</i> sp.	T: UMC; H: UMS
<i>Diaeritus rapae</i> (Curt.)	T: UMC
<i>Trioxys</i> sp.	S: AS
<i>Doryctes</i> sp.	T: UMS
<i>Goniocormus</i> sp.	T: UMC
Serphoidea	
<i>Trichopria</i> sp.	T: AS
<i>Calliceras</i> sp.	S: LMC
Dryinidae	
<i>Anteon</i> sp.	H: AS
Ichneumonidae	
<i>Cratichneumon adonis</i> Vier. ?	H: AS
<i>Amblyteles</i> sp.	S: UMS
<i>Amblyteles brevipennis</i> (Cress.)	G: AS
<i>Phaeogenes</i> sp.	H: AS; S: UMC

<i>Cryptus altonii</i> D. T.....	H: AS
<i>Cryptus coloradensis</i> Ashm.....	S: AS
<i>Phygadeuon</i> sp.....	S: UMC; H: UMS
<i>Aclastus</i> sp.....	S: LMC; H: UMC. UMS
<i>Hemiteles</i> sp.....	S: LMC
<i>Itoplectis obesus</i> Cush.....	T: UMS
<i>Lissonota</i> sp.....	S: AS
<i>Alexeter</i> sp.....	H: UMS
<i>Diplazon pulchripes</i> (Prov.).....	H: UMC
<i>Orthocentrus</i> sp.....	H: LMC; T: UMC
<i>Camptoplegidea pilosa</i> Walley.....	T: LMC
<i>Angitia</i> sp.....	H: AS
<i>Inareolata eureka</i> (Ashm.).....	S: LMC
<i>Camptoplex</i> sp.....	H: UMS
<i>Leptopygus politus</i> (Ashm.).....	S: AS
<b>Cynipidae</b>	
<i>Melanips</i> sp.....	H: LMC
<i>Hexacola</i> sp.....	S: UMC
<i>Phaenoglyphis</i> sp.....	T: AS
<i>Charips</i> sp.....	T: UMC
<i>Ceroptres</i> sp.....	S: LMC
<b>Chalcidoidea</b>	
<i>Amblymerus</i> sp.....	T: UMS
<i>Haltioptera stella</i> Gir.....	H: UMS; S: UMS; T: UMS
<i>Zatropis</i> sp.....	H: UMS
<i>Pteromalus</i> sp.....	H: AS
<i>Habrocytus</i> sp.....	S: AS
<i>Syntomopus americanus</i> Ashm.....	S: UMS
<i>Asaphes californicus</i> Gir.....	T: UMC
<i>Terobia</i> sp.....	T: UMC
<i>Terobia</i> sp.....	H: UMS
<i>Terobia</i> sp.....	H: UMS
<i>Parerotolepsia</i> sp.....	H: UMS
<i>Bothriothorax californicus</i> How.....	H: UMS
<i>Microterys</i> sp.....	T: UMS
<i>Berecynthus bakeri</i> How.....	T: UMS
<i>Eupelmus</i> sp.....	T: UMC
<i>Pseudochalcura</i> sp.....	S: LMC
<i>Elachertus</i> sp.....	T: AS
<i>Elachertus</i> sp.....	S: LMC
<i>Elachertus</i> sp.....	H: AS
<i>Elachertus</i> sp.....	T: AS
<i>Callimome</i> sp.....	H: UMS
<i>Callimome</i> sp.....	H: AS; S: LMC; T: AS
<i>Callimome</i> sp.....	H: UMS; S: UMS
<i>Callimome</i> sp.....	T: UMC
<i>Callimome</i> sp.....	H: LMC
<i>Megastigmus</i> sp.....	S: LMC
<i>Cryptopristus lazulella</i> Ashm.....	H: UMS



<i>Spilochalcis albifrons</i> (Walsh) .....	H: AS
<i>Platygaster</i> sp. ....	H: AS
<i>Megaspilus</i> sp. ....	H: AS; T: UMC

## APPENDIX C

A partial list of the Lepidoptera found on Mt. Timpanogos, Utah:

## Papilionidae

*Papilio bairdii hollandii* Edw.

*Parnassius clodius* Men.

## Pieridae

*Colias eurythema* Bdv.

*Colias eurytheme eryphyle* Edw.

*Pieris occidentalis* Reak.

*Pieris occidentalis calyce* Edw.

*Pieris rapae* L.

*Pieris napi* L.

## Nymphalidae

*Minosis oetus* Bdv.

*Argynnis nevadensis* Edw.

*Argynnis chitone* Edw.

*Argynnis utahensis* Skin.

*Argynnis pfoutsi* Gund.

*Euphydryas chalcedona* Dbldy, and Hew.

*Nymphalis californica* Bdv.

*Nymphalis milberti* Godt.

*Basilarchia weidemeyrii* Edw.

*Vanessa cardui* L.

*Vanessa carye*, Hbn.

## Lycaenidae

*Lycaena heteronea* Bdv.

*Lycaena rubidus* Behr.

## Sphingidae

*Sphinx chersis* Hbn.

*Celerio lineata* Fabr.

## Pericopidae

*Gnophaela lapipennis vermiculata* G. and R.

## APPENDIX D

## Gazetteer of Stations

(Map, Fig. 1)

(No quantitative work was done at stations A, B, C)

**Station 1.** Lower Montane climax coniferous forest, Aspen Grove, 4.85 miles northwest of Wildwood Resort, Mt. Timpanogos, Utah

County, Utah. Elevation 6,800 feet. Located in township 5S, range 3E, section 9. All geographical locations are given with reference to the Salt Lake meridian.

**Station 2.** Aspen subclimax of the Montane Forest, Big Tree Camp, 3.2 miles northwest of Aspen Grove, Mt. Timpanogos. Elevation 7,700 feet. Located in township 4S, range 3E, section 33.

**Station 3.** (Not shown on map) Upper Montane climax, Lost Lake Forest Camp, longitude about  $110^{\circ} 37'$ , latitude  $40^{\circ} 41'$ , Wasatch-Summit County line. Elevation 9,800 feet. A land survey marker near the area shows the corners of sections 32 and 33, township 1S, range 9E, and sections 4 and 5, township 2S, range 9E Salt Lake meridian.

**Station 4.** Upper Montane subclimax, Timpanogos Cirque, near Hidden Lake, Mt. Timpanogos. Elevation 9,700 feet. Located in township 5S, range 2E, section 8.

**Station 5.** Chaparral Ecotone, southwest-facing slope, directly across the canyon from station 1. Located in section 3.

**Station 6.** Alpine Meadow, Timpanogos Cirque, located about a half mile southwest of station 4. Elevation about 10,000 feet.

**Station A.** Chaparral ecotone, between Dry and Battle Creek Canyon, west side of Mt. Timpanogos, elevation about 6,000 feet. Located in township 5S, range 2E, section 23 and 26.

**Station B.** Chaparral ecotone, mouth of Grove Creek Canyon, west face of Mt. Timpanogos, elevation about 5,200 feet. Located in township 4S, range 2E, section 15.

**Station C.** Aspen subclimax, Camp Timpooneke, 7.17 miles northwest of Aspen Grove, Mt. Timpanogos, elevation about 7,300 feet. Located in township 4S, range 3E, section 30.

## A NEW SPECIES OF *ARAEOSCHIZUS* (Coleoptera-Tenebrionidae)

VASCO M. TANNER<sup>(1)</sup>  
Professor of Zoology and Entomology  
Brigham Young Univeristy

### *Araeoschizus airmeti* Tanner, new species

Form robust, moderately convex, uniform dark red-brown in color; head large, longer than wide, widest at anterior third, the sides from the antennae slightly converging and arcuate to the basal angles, which are definitely rounded, the base broadly truncate, the occiput definitely impressed at the extreme base; surface above and beneath coarsely and densely punctate and moderately shining, the fulvous squamules conspicuous on all parts of the body, especially on the margins and ridges of the head, prothorax, and elytra; eyes divided and elongate, with five facets below on each side and nineteen on each side above; prothorax widest anteriorly, where the sides are evenly rounded, thence strongly converging down to the base and apex, base one-half as wide as the anterior third, sides with dense erect fringe which extends to the apex and base, being slightly clumped at the base, the surface with a broad shallow sulcus from the base to the apex, long erect squamules along the base, being parted at the sulcus, punctation similar to head surface but more closely set than beneath; elytra one-third longer than wide, twice as wide as the prothorax, oval, the sides strongly rounded at the base but only gradually behind, five strongly elevated ridges on each elytron, between the third, fourth, and fifth ridges are two deeply punctured series of the intervals separated by a scarcely elevated line of squamiferous punctures similar to those of the ridges, these scarcely elevated lines do not reach the base and do not extend much beyond the declivity at the apical end, the deep punctures of the intervals do extend to the apex although they are smaller and more closely set; abdomen shining, finely punctured with sparse setae except on the apical sternite and posterior margins of the other sternites which bear similar yellowish squamules, as are found on other parts of the insect; legs with a covering of decumbent vestiture, femora with a small acute denticle beneath beyond the middle, the posterior femora are less denticulate than the anterior ones, yet a small denticle is present.

Length 4.5 to 4.9 mm; width 1.6 to 1.7 mm.

TYPE LOCALITY: Nampa, Canyon County, Idaho. Collected in April, 1944 by Elliot LeRoy Jack Airmet, a student of Entomology at this institution, and in whose honor the species is named. One other specimen of the series was collected in the Juniper Hills near Rexburg, Idaho in May, 1919, by Ernest Quayle. The type and thirteen paratypes in the entomological collections at Brigham Young University.

REMARKS: This is the largest tenebrionid of this genus thus far reported. Its size, body proportions, denticles of the femora, and

(1) Contribution No. 109.

punctuation of the elytra serve to separate it from Col. Casey's *duplicatus* and Horn's *armatus* with which it is closely related. This species was found associated with ants. In February, 1924, I collected specimens of *regularis* Horn at Saint George, Washington County, Utah in the nests of ants of the genus *Aphaenogaster*.

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### Some Corrections in *Hesperotettix*

Since the publication of my paper on "The Genus *Hesperotettix* in Utah" (Great Basin Naturalist, Vol. III, No. 1, 1942) I have submitted all my specimens of *Hesperotettix pacificus* Scudder to Morgan Hebard for determination and he has determined them to be *Hesperotettix viridis terminus* Hebard. It is a serious oversight that I did not submit my material for determination before publication. I really thought I had done so, but this particular species had escaped. The discussion in the paper referred to, which comes under the heading *Hesperotettix pacificus* Scudder, should really be headed *Hesperotettix viridis terminus* Hebard. The synonymy for *pacificus* should, of course, be omitted.

The spelling for *H. viridis terminus* Hebard is erroneous in the paper. It should be *t-e-r-m-i-n-u-s* and not *t-e-r-m-i-n-u-s*.—W. W. Henderson.



### Water Birds Observed at Rock Island, Utah Lake, in 1932

In a recent article on the natural history of the California Gull (*Larus californicus*) based on studies at the Rock Island colony at Utah Lake, Beck (Great Basin Nat., 3, 1942: 91-108) mentions (p. 93) the findings of some previous visitors to the island. These early observations are none too numerous and it has seemed desirable, therefore, to place on record certain data gathered by the writer on a visit to the same site on May 26, 1932. Accompanied by John W. Sugden and A. M. Woodbury the boat was launched at the mouth of the Provo River and a landing was made at an indentation on the north shore of the island. A strong wind was blowing at the time, causing large waves. The wind seemed to be increasing in velocity and being apprehensive about the return trip, our stay on the island was of short duration, which permitted only hurried observations. Even so, the following species were seen or evidence was found of their presence.

*Pelecanus erythrorhynchos* Gmelin. White Pelican. Over 100 white pelicans were gathered in a flock at the tip of a long sandbar extending shoreward from the south end of the island. They remained there "loafing" throughout the time of our visit. These birds were probably affiliated with one of the Great Salt Lake colonies, for although a pelican colony was once situated at Rock Island (Goodwin, Condor, 6, 1904: 126-129) the island has apparently long been abandoned by pelicans as a nesting site. However, pelicans are fairly common at Utah Lake which is, or used to be, one of the principal foraging areas for the pelicans of Great Salt Lake.

*Phalacrocorax auritus auritus* (Lesson). Double-crested cormorant. Six cormorants were seen in flight past the island. As in the case of the pelicans, cormorants do not nest on Rock Island, but Utah Lake is a foraging ground for the Great Salt Lake birds.

*Branta canadensis canadensis* (Linnaeus). Canada Goose. No birds were seen but two nests were found, both of which had been abandoned as indicated by the putrifying contents of the eggs. One nest had 3 eggs, the other 1 egg.

*Anas cyanoptera cyanoptera* (Vieillot). Cinnamon Teal. An adult was flushed from a nest which contained 12 eggs.

*Charadrius vociferus vociferus* (Linnaeus). Killdeer. Several killdeers were seen scattered about the island and one nest was found with a full complement of 4 eggs.

*Actitis macularia* (Linnaeus). Spotted Sandpiper. Twelve were seen on the island, of which one was collected.

*Crocethia alba* (Pallas). Sanderling. A flock of 50 or so was seen, 4 of which were collected.

*Recurvirostra americana* Gmelin. Avocet. Ten avocets were at the island, but no nests were found.

*Larus californicus* Lawrence. California Gull. An estimated 2000 were on or around the island. Their nesting area was on the north and west sides of the island. The nests had 1 and 2 as well as 3 eggs indicating that the laying period was then in progress. The nests were spaced about 5 feet apart and were sub-

stantial structures as compared with those on the islands of Great Salt Lake where there is less nesting material for the more abundant population.

*Chlidonias nigra surinamensis* (Gmelin). Black Tern. Six individuals were seen but there was no evidence of their nesting.

*Hydroprogne caspia imperator* Coues. Caspian Tern. A colony was located on the northwest part of the island. The number of nests was established as about 50 with adults numbering not more than 100. Most of the nests had 2 or 3 eggs, but one contained 5. Several eggs had been laid outside nests. California gulls nested all around the Caspian Tern colony.

*Sterna forsteri* Nuttall. Forster Tern. Two colonies were found, a relatively small one at the northern point of the island and a second larger one more toward the center of the island. Nests were numerous, but seemingly less so than the old nests of the previous season. The number of eggs in the nests varied from 1 to 3. There were about 500 adults on the island.—William H. Behle, University of Utah, Salt Lake City, Utah. March 15, 1944.

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### The Plant Clear-eye or See-bright a New Record for Utah

On July 22, 1945, Louise Atkinson and I discovered the Clear-eye or See-bright *Salvia sclarea* growing in Emigration Canyon, Salt Lake County, Utah. This member of the mint family is found in Pennsylvania, and so far as we know has never before been taken in Utah.

We found the first clump at 5025 ft. altitude, 1.6 miles up the canyon from the road junction at its mouth; the second, at 5100 ft., 2.3 miles; the third at 2.7 miles; the fourth at 3.3 miles, altitude 5225; and the fifth and largest at 3.6 miles, altitude 5250 feet. At this last point there were probably a thousand plants on the north hillside, all with their clusters of pinkish white flowers in terminal spikes. The broad, ovate bracts furnish the color.

All of these plants were growing on sunny north slopes on good soil, preferably that recently eroded or graded. We are indebted to Prof. A. O. Garrett for assistance in the final determination of this species.—Claude T. Barnes.

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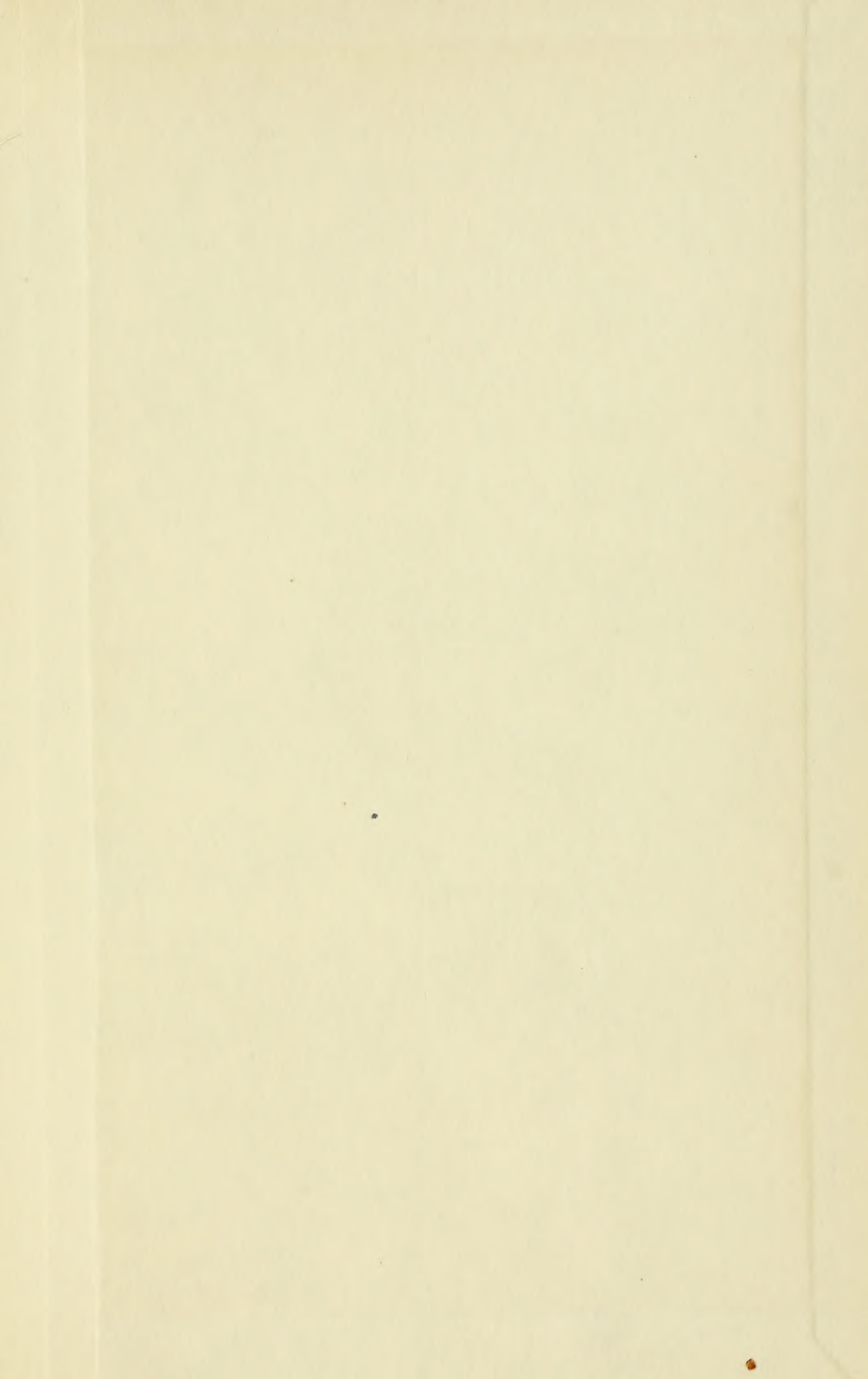












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